ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

ERRATA

May cover, last line of Contents—186 should read 184.

Page 65, line 29—var. nov. should read sp. nov.

Page 113, line 34, and on following pages of Gage's paper—*chinensis* should read *chinense*.

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TABLE OF CONTENTS

		PAGE
Bluegrass Pasture Almanac	Alfred G. Etter	1– 30
The Popcorns of Turkey	Edgar Anderson and William L. Brown	33– 48
A Preliminary Survey of the Milpa System of Maize Culture as Practiced by the Maya Indians of the Northern part of the Yucatan Peninsula	R. A. Emerson	51– 62
A Contribution to the Lichen Flora of Arizona and New Mexico	Emanuel D. Rudolph	63– 72
The Analysis of Suspected Hybrids, as Illustrated by *Berberis* × *gladwynensis*	Edgar Anderson	73– 78
Variation in Cob Morphology among Certain Archaeological and Ethnological Races of Maize	Norton H. Nickerson	79–111
The Cytology, Morphology, and Systematic Relationships of *Delphinium* × *Belladonna* Hort. *ex* Bergm.	Marilyn Amy Gage	113–182
Some American Medullosas	Henry N. Andrews and Sergius H. Mamay	183–209
The Distribution of *Diospyros virginiana* L.	Harry R. Skallerup	211–225
Wildwood—A Study in Historical Ecology	Alfred G. Etter	227–258
Some X-Ray Effects in *Petunia*	Henry A. McQuade	259–270
Some Lichens of Tropical Africa	Carroll W. Dodge	271–401
General Index to Volume XL		403–412

Volume XL Number 1

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Vol. 40 FEBRUARY, 1953 No. 1

BLUEGRASS PASTURE ALMANAC*

ALFRED GORDON ETTER

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Washington University School of Medicine

JANUARY

The long summer leaves of bluegrass have turned brown, making the sere meadows and pastures of winter. In a few places, however, where these long leaves have been grazed off, pastures are still rather green. Bluegrass is also surprisingly green under certain trees and on the north slopes of hills. Isolated plants and small clones beneath apple trees in the orchard are brilliant green and are used by rabbits in preference to the tangle of brown plants in adjacent sod in full sun. Shading produces plants with leaves proportionately high in protein and low in fiber, which seem to satisfy the cottontails. Shading also restricts rhizome development sufficiently so that plants do not become crowded and thus sod-bound and nitrogen-deficient. After tree leaves are shed in fall, plants that were shaded all summer stay green well into the winter. When blades of these plants do die, they wither into very thin and delicate tufts, low in fiber, that contrast with the tough persistent dead leaves of sun-grown plants.

Hogs on the hill pasture are working up moist areas into black patches of open soil. Where a bed of limestone outcrops above a bed of shale there are seeps which keep the ground soft and wet. Hogs have made the contact of these two formations clearly visible across the hill (fig. 1). Their trails across the orchard-grass

* The observations recorded in this study were made during the writer's three-year residence on Brookhill Farm, near Clarksville, Missouri. This farm and funds for a special research fellowship were given to Washington University by the late Dr. Malvern B. Clopton, whose abiding interest was in the relation of living things to the land. Grateful appreciation is due Dr. Edgar Anderson of the Henry Shaw School of Botany of Washington University, and Dr. Arthur H. Compton, Chancellor, for arranging this unusual opportunity for the author. Much credit is also due the late Prof. Aldo Leopold of the University of Wisconsin, whose inspiration provided a background for these studies. A generous grant from the O. M. Scott & Sons Company of Marysville, Ohio, has made it possible for the author to organize his field notes and prepare the almanac for publication. The present paper is a companion study to the author's "How Kentucky Bluegrass Grows," which appeared in the September issue of the ANNALS for 1951 (Vol. 38, pp. 293–375). References to the morphology and growth habits of bluegrass will be made much more clear by referring to some of the diagrams in that paper.

pasture are also very apparent now. In a part of this pasture which was left unmowed, the orchard-grass plants became rank and have been avoided by the hogs, not only in their feeding but also as they walk about the pasture. Consequently the pasture there has deteriorated into a rough tussocked run (fig. 2).

During winter when the ground remains frozen for long periods, bluegrass leaves become thin, wiry and twisted, with tips curving inward, probably as a result of the difficulty of obtaining moisture from the frozen soil. January leaves are very short, only an inch or so long. In areas closely grazed since fall, stock are hard-put to it to find enough to eat. Horses are able to eat close enough, but hay is being fed cattle.

The grazing habits of stock are distinctive and play an important role in determining the appearance of a pasture throughout the year. An important fact is that cattle and horses prefer grass which has grown in soil fed by the nutrients contained in their urine. They instinctively conserve the nitrogen, potassium, phosphorous, and trace minerals that urine contains and benefit from the stimulation which these substances, as well as dissolved hormones and vitamins, give the soil microorganisms and the herbage itself. This they do by actually seeking out the deep green grass which grows where urine has fallen (figs. 7 and 11). Analyses made by the author of grass in these spots has shown that it contains twice as much vitamin A (carotene) as ordinary grass, and Neven (1941) reports that the protein content of such fertilized grass may be nearly doubled.

Horses graze small areas intensively, but cattle range widely. Urine is distributed as the animals graze so that characteristic patterns of urine-fertilized grass develop. The pattern produced by cattle seems to be a rather random distribution over the pasture as a whole. With horses, however, urinations occur in small areas where the grass is kept closely grazed (fig. 7). The urine characteristically falls either on this short grass or, when grazing pressure increases, along the edges of these grazings (fig. 12) in which case it has the effect of continually enlarging the intensively grazed area (fig. 13).

Of equal significance is the distribution of manure. Stock avoid grass around their own manure clumps as instinctively as they seek out that fertilized by their urine. Cattle manure is scattered rather indiscriminately though there is some considerable concentration in loafing and bedding areas. Horse droppings, however, are somewhat controlled and deliberately concentrated in certain spots around the pasture. Often these spots are low places or fence corners; almost invariably they are weedy, full of rank vegetation. By keeping the manure thus concentrated and out of the way, their system of intensive grazing on small urine-fertilized areas is not interfered with.

Since in summer, stock avoid grass around clumps of their own manure, "rough" areas of rank grass are protected from consumption (figs. 9 and 13). Considerable forage is thus saved for winter use. When the manure is frozen it no longer seems to be objectionable. In January, when new grass growth is at a

minimum, these areas are brought into use. Clumps of manure previously protected by grass are now exposed, and to some extent are being scattered about the pasture. These "roughs" provide a convenient emergency supply of fodder when freezing rains and sleets fall. Urine grazings become a solid sheet of ice, but roughs, drifted with a little sleet, are still rather soft underfoot, and horses can paw them with their hooves, scrape away the crust of snow, and obtain all the grass they need (fig. 3). Cattle are not quite so adaptable and must be fed. No matter how heavy summer grazing may be, reserves of long grass around manure will usually be saved for overwintering. If fall months are very dry, however, grass growth will be slow throughout the pasture and "rough" reserves will be invaded during October and November so that before winter is over roughs may almost disappear.

The past summer certain small blocks of pasture were enclosed with fence so that stock could not reach the grass within them (figs. 1 and 10). This protected grass has grown rank, and I can be almost certain that in each "exclosure" a rabbit will be spending the day. In fall and winter rabbits like the rich proteinaceous grass nourished by stock urine. By using these protected islands in the pasture they have access to much of that fertile grass, and their pellets are often found in closely grazed urine grass.

The rabbit's midwinter desire for proteinaceous food, which apparently accompanies the advent of the breeding season, is satisfied by grazing intensively small plots of grass which have been fed urine by dogs, stock, man, or by the rabbits themselves. These grazing places are eaten down into the dirt with nothing but bare soil remaining (fig. 4). Such rabbit pastures are common sights along the runways of rabbits in winter orchards. They can also be seen occasionally in the summertime (fig. 20).

In some places mice grazings are just as conspicuous. In October some urine was poured in a circle around a stake placed in an old Canada bluegrass meadow. Now the grass which received urine has been completely consumed and the ground is bare in a circle around the post (fig. 5). Even the rhizomes have been eaten. More striking still, where some of the urine had fallen on the post, the wood was chewed up by the mice.

Gophers are no longer busy bringing up their piles of dirt as they were during fall (fig. 6). The extensive bulldozing they did then is slumping down with the frost and being scattered by treading hooves and being undermined by rhizomes of bluegrass. Most fall gopher mounds are built after temperatures are low enough to keep weed seeds from germinating. Also in fall and winter rhizoming and tillering of bluegrass are very active, and the new loosened aerated soil in the mounds encourages the vigorous vegetative development of bluegrass plants around its edges. The invasion and conquest of the mound go on to some extent all winter, for the loose soil does not freeze deeply. Revegetation of these mounds is

also accomplished by plants which have been buried beneath the soil. When leaves and crowns are covered, internodes elongate and bring the crown up to the surface of the mound. Branching of rhizomes, while infrequent in most places, is the order of the day in gopher mounds.

February

Wherever the pasture thaws during the winter, stock cut the sod with their hooves and create large scars by sliding and slipping. These scars usually heal rapidly if made in early winter, but may remain for a considerable period if made in late spring. When the snow is soft, horses moving about build up pads of snow on their hooves. When these pads later slip off, many weed seeds and even vegetative parts are carried about and planted. From a single pad picked up in February, 28 plants were germinated. Sixteen species were represented, half of which were grasses (Etter, 1948).

During these cold months the rhizomes of bluegrass which began to grow in late October and November behave much as do the bulbs of such early spring plants as jonquils. Being situated near the surface of the soil, however, they are more subject to variations in the weather. They grow slowly in late fall, fitfully with thaws in the winter, and rapidly in the spring, shooting up and developing into new plants. At any time in winter one may find, in places where growth is rather vigorous and fall grazing was not too intensive, small rhizomes which are all white. Those which did considerable growing in fall have slightly green tips, and others may show a few short leaves.

The dominant process, of course, during winter in every bluegrass plant is tillering. In old meadows this proceeds at a snail's pace, but along streams, in loose, rich soil, where plants have room to stretch and root, it proceeds rapidly. More subtle is the secret development of the bluegrass seed head within enclosing sheaths. This process may have begun as early as November or may wait as late as March, depending on variety and environment.

Winter thaws are important to bluegrass. With only a little rise in the soil temperature above freezing, fat white roots develop from the new tillers which have originated during the previous months. These roots, in turn, appear to stimulate new buds to develop into additional tillers. Where the soil is protected by an overburden of long leaves, thawing is slower and less frequent and roots do not develop very rapidly. Well-grazed or isolated plants, however, begin to send out roots a few hours after the soil thaws. This may play an important part in the earliness and the more vigorous growth of open-grown or spaced plants often observed along paths, in alluvium, in gardens, or near buildings. It is certainly true that bluegrass is often early to flower on the south sides of buildings and hills, above subterranean steam pipes, under eaves that drip warm water frequently in winter, or in places that are protected from snowdrifts as on the south sides of evergreens.

In meadows, now, there are well-camouflaged tunnels through which mice circulate in contempt of the winter weather. These are not mere pathways to and from, but feed alleys along which mice find their food. The stems of grass are cut near the ground to make the tunnel. When new leaves grow from the crowns of these severed plants, they stick up along the pathway. This growth is tender, bleached, and proteinaceous and is nipped off by the mouse as he navigates his pasture. These tunnels occur in heavy meadow grass where the overburden of leaves keeps the soil from freezing deeply, so that a small amount of blade growth takes place throughout the winter. Small feeding pockets extend short distances from the tunnels and are frequently filled with the grass-green pellets of mice. Undoubtedly the urine is also there. The floor of the tunnels and pockets is littered with clipped stems and pellets and is penetrated by a maze of bluegrass roots. When the ground thaws, the pellets disintegrate and a rich bed of mold develops, fed by these excretory products. The reserves of the rhizomes and crowns which feed the grazed plants are depleted by winter-long grazing and lack of sun, and tend, in spring, to produce weak growth which is often unable to reach through the overburden to the light.

When plants such as chicory and plantain, which have bulky storage crowns, grow isolated in rank meadows they are apt to be consumed over winter by mice or gophers. Two plants, one of plantain, one of chicory, which I had marked last summer have been cut down and their roots consumed and transformed into a pile of pellets.

March

A little warm weather in late February and March is soon followed by a slight greening-up of pastures. Earthworms return to the topsoil and robins arrive in time to take advantage of them. Flocks of starlings and purple grackles are often found feeding on these early spring pastures.

During December and January bluegrass leaves tend to become short and prostrate, and leaves grow only about a half centimeter a week. When the days become longer and thaws are frequent, leaves and plants straighten up. New leaves shoot up from tillers and rhizomes which have developed during the winter. Since the snow, ice, wind, and treading cattle have broken the old tufts of grass in much of the pasture, these new leaves are not encased in the long sheaths of the previous year, and so become visible almost as soon as growth begins. Where leaves reach the light with a minimum expenditure of food reserves, they are inclined to be more vigorous, broader, deeper green, and more attractive to livestock than those which have had to struggle up to find light. During this greening-up period, little further tillering occurs, and this is one time of the year when virtually no rhizomes are initiated. Any rhizomes still underground turn up and proceed to develop leaves. Often after this green-up first begins, the weather becomes cold again and leaf blades become reddish at the tips and growth almost stops. This redness, apparently anthocyanin accumulation, is especially common in the

tips of grass recently grazed or cut. It seems to be a characteristic response of plants which are all ready to begin active growth and are prevented from doing so, either by injury, drought, low temperature, or excessively bright sun.

During this spring renaissance, reserves in the crown, roots, and rhizomes are used up to produce new leaf growth. Sods become remarkably weak and may be pulled apart more easily than at any other time.

Wherever urine has fallen on the soil since last September, bluegrass shows an early difference. Grass fed nitrogen does much more growing at low temperatures, below 40°, than does unfertilized grass (Blackman, 1936). At higher temperatures the nitrogen seems to have relatively less effect. Urine-fertilized grass is deeper green, thicker, and broader-leaved. Growth is also early in other sites where the ground is rich or moist, such as bare places once occupied by haystacks, near manure piles, in seeps, and around the edges of spots of sod burned out by urine last summer.

Now that the sod is becoming soft, hogs are taken off the permanent pastures. Where they have been fed is a litter of corn cobs and mud which will become a rank bed of rich weeds in a few months.

Horse grazings are now strikingly differentiated from the rest of the pasture which still is rather bleached (fig. 7). Tufts of grass fed by steer urine during fall and winter are now becoming visible, and cattle run in these early pastures seek out these patches. It is interesting that horse urine does not burn bluegrass when it falls on frozen ground. By mid-March, however, severe burning may occur. Cattle urine seldom burns grass even in mid-summer.

APRIL

In early April dormant buds on the bluegrass crown begin to swell, anticipating the spring flush of rhizomes that accompanies flowering. At the same time, bluegrass florets and panicles are growing, getting ready for the grand elongation of the stem which will occur in a few weeks. Long green blades of bluegrass are waving in the wind. Where pastures were not grazed last fall the blades are long, three or four inches, while in grazed places they are only an inch or so long and form small rosettes. There are many more blades in the grazed area, however. In rich soil, closely grazed, there may be twenty or more blades to a square inch.

Trails and paths made through old meadows last summer and fall show up conspicuously now as stripes of green grass in a tangle of old whitish leaves. Breaking down the sheaths and shading growth gave short fall and winter leaves access to winter sun. This stimulated tillering. A rough count of leaves along such a pathway showed twice as many new spring leaves as in undisturbed parts of the field. This path was used only one day, when it was walked over only five or six times. It demonstrates very simply how fall discing or mowing and raking of neglected pastures will do much to improve them.

Down along the creek the succession of plants on newly built alluvial banks leads eventually, under grazing, to bluegrass. After gravel bars are stabilized by

sweet clover (*Melilotus officinalis* L. (Lam.), bouncing-Bet (*Saponaria officinalis* L.) and willow sprouts, coatings of alluvium begin to support a variety of weeds. Composites such as species of bur marigold (*Bidens* sp.), cocklebur (*Xanthium* sp.), sunflower (*Helianthus* sp.), as well as great ragweed (*Ambrosia trifida* L.), will also grow here, but will not withstand grazing and trampling. Rhizomes of *Muhlenbergia racemosa* (Michx.) B.S.P., broken loose from clones upstream, lodge on banks and begin to establish a rank stand of coarse grass which ties down the soil and speeds up deposition. As time goes on, bluegrass becomes established and invades and eliminates the other species. Without grazing, the succession would proceed from the coarse grass and weeds to shrub and tree growth. Grazed alluvial banks support excellent stands of bluegrass in the older established areas.

Other grasses are developing rapidly now. Orchard grass (*Dactylis glomerata* L.) is flowering, and quack grass (*Agropyron repens* (L.) Beauv.) and smooth brome (*Bromus inermis* Leyss.) are beginning to develop rhizomes, while Canada bluegrass (*Poa compressa* L.) sods, devoid of new leaves, show many long white rhizomes which have not yet turned up. Redtop (*Agrostis alba* L.) is still almost dormant, a few green leaves beginning to appear. Purpletop (*Triodia flava* L.) has made virtually no growth, although its white dead stems are prominent in parts of certain pastures (fig. 8). On south slopes dandelions are just appearing, and in thin places a variety of small seedlings now appear. Old chicory (*Cichorium Intybus* L.) plants show only a few small leaves.

Earthworms are abundant and are throwing up extensive castings within the secrecy of the grass. This subtle cultivation, accompanied by an increase in the numbers and activity of nitrogen-fixing bacteria in the soil, comes at the time when bluegrass needs it for rapid nitrogen-consuming leaf growth and inflorescence development. Moles are busy now too, tunneling in well-drained places, but gophers seem strangely absent. Cottontail rabbits are using wads of last summer's long grass to hide their nests in. Young cottontails will be venturing from these nests very soon.

By mid-April the blades on the flowering shoots of bluegrass have finished their development, but they are still telescoped within each other, waiting for the elongation of sheaths and internodes. The panicle or flowering head can be found just within the sheath of the newest leaf. It is striking to note that shoots of bluegrass which are going to bloom this spring can be easily selected now, because they have shorter and wider leaves than the blind or non-flowering shoots, and they are conspicuously a deeper bluer green.

The short winter leaves are beginning to turn yellow, and this dulls the greenness of the pasture very slightly. When stock graze the pastures now they are getting not only leaves but the developing flowers within. Mowing or close grazing at this time will greatly reduce the flowering of pastures. It will also produce a silage or feed as rich in protein as bluegrass can produce. It may, however, be a little short on sugar. By waiting a few weeks for the panicles to develop

a little further a heavier yield will be forthcoming and the carbohydrate content will increase, though the per cent protein will drop accordingly.

Old gopher mounds are now drying out and are very evident in pastures grazed continuously, for the grass there has not been given much chance to cover them (fig. 6). Bluegrass plants which grow on these mounds are very distinctive; the leaves are short and wide, deep blue-green, are prostrate, and often have much anthocyanin in their blades. Flowering shoots are consistently early to appear and grow almost horizontally.

Winter pigs are on pasture now and they thrive on the high protein of the new grass. They are also busy rooting for worms and other foods in the loose soil under walnut trees. In a few weeks they will be seeking clover. Where hogs were pastured during the cold months, what grass remains is now a brilliant green. Hog urine has an especially strong, though brief, effect on bluegrass, and that combined with the well-distributed manure and treading stimulates the grass as it is stimulated in few other places.

The excretory behaviour of swine is quite as interesting and significant as is that of cattle and horses. Hogs, when penned, are very careful to drop their manure only in certain corners. When on pasture they are careful to keep both urine and manure from contaminating the bedding area. Consequently, both waste products accumulate just outside the sleeping area, where sleepy hogs politely retire. Swine are just as careful not to defile their rooting areas, although here the prejudice is limited to the solid droppings. They do not hesitate to urinate in their excavations or in their wallows. Since hogs have need for various trace elements and antibiotics, it is quite possible that wallowing may be more than merely a way of keeping cool. The continual dabbling and rooting and munching that goes on while pigs search their wallows may provide them in a natural way with nitrogen, animal protein factors, and trace elements.

Almost invariably, after rooting and wallowing, hogs leave along some much-used path, travel a few hundred feet, drop dung just off the path, and proceed with the day's affairs. Where pastures are intensively grazed and where corn supplements, minerals, and water are provided all close together, these patterns are broken down and feeding areas are littered with manure. Frequent worming then becomes a necessity.

In a pasture grazed last fall for a few months by steers at a rate of about two head per acre, there now appear as many as 20 urine spots in a plot 45 feet square, or about 1 square foot of urine grass to 40 unfertilized. In a pasture grazed longer and more intensively the spots are so close that I can easily step from one to the other. An important result of the stimulation of these pastures by urine is that bulky and less nutritious plants which might ordinarily be avoided are consumed to provide the necessary bulk. It is a common observation that the more rich proteinaceous food an animal has the more bulk it can handle.

It is rather easy to tell approximately when the urine fell which stimulated a certain piece of sod, for the vegetative response to fertilization depends on the season when it is applied. Urine applied in fall promotes vigorous tillering which leads to short leaves and many short inflorescences with heavy loads of flowers and a decided blue-green color. Spring applications produce leaves as long as the inflorescences. These shoots are weak, short, bear few well-developed flowers, and often lodge. With such information it is possible by examining urine spots to tell approximately when and how long an area was grazed. It is interesting that pig and calf urines have no such effect as do hog, beef, human, or mare urines. The difference in the reaction of the grass may be due partly to the characteristically lower nitrogen content of urine from a growing animal, or to a different hormonal content.

The effect of urine on the grass of pastures is not limited to a single season, although the striking flush of growth in spring is the response most commonly seen. There is a more lasting influence as a consequence of the fact that urine stimulates the development of grasses more than it does of weeds, especially when applied in winter. This rapid growth smothers out weed seedlings, clover plants, and results in a pure stand of bluegrass. Urine holds down weed development in a second way. From controlled tests made in flats kept in a greenhouse and planted to a variety of pasture weed seeds and grasses, it was found that germination of weed seeds was strongly inhibited in flats treated with urine, while grass seeds suffered little if any such inhibition. This effect was just as marked when urine was applied to plots of bluegrass in the pasture or on a lawn (fig. 14).

In pastures grazed last summer by the horses there is much clover. Horse pastures characteristically contain more clover than those grazed by cattle. This is due in part to four facts: (1) Close grazing encourages clover, and horses graze quite close. (2) Compaction of the soil in certain areas maintains a favorable moisture condition for germination. (3) Breaking of the sod during winter induces germination of clover seeds, and horses cut the sod more than cattle. In a simple chopping test where a rank sod of pure bluegrass was cut with numerous strokes of a hand axe while the ground was frozen, clover germinated the following spring to such an extent that boundaries of the plot could easily be discerned. Winter discing also favors clover. (4) Most interesting relationship of all, however, is that involving urine and grass. Horse urine that falls on growing grass usually kills it; cow urine does not. Burned patches soon become bare ground. While weather and soil conditions influence the flora that develops on these spots it is especially characteristic that spots which develop in dry mid-summer or fall remain bare until the following spring. At that time clover seedlings take over the bare ground and by April the patches are solid in clover. The attraction which urine-saturated soil has for earthworms and many other burrowing organisms may lead to extensive aeration of these spots and so encourage clover germination also.

By the last week in April dandelions and peppergrass (*Lepidium virginicum* L.) are beginning to elongate, having already produced nutritious rosettes. Not only

has bluegrass begun active production of rhizomes, but the panicles of early-flowering bluegrass plants have already been exserted. Silica deposition in the soft culms is going on and stock are avoiding them now. Where grazing is close and intensive the tough stem interferes with the efficiency of the grazing procedure. The stem does not tear when the cow pulls on the leaves, but instead the entire plant comes up by the roots. Dead plants pulled up in this manner litter the turf in places.

At this season when growth is more rapid than at any other, a surplus of herbage soon develops and stock begin to pick and choose their preferences. A striking example of the attraction which urine-fed grass has for cattle now is shown in fig. 11.

May

During the first part of May flowering stems of bluegrass elongate rapidly, at least a centimeter a day. Ungrazed pastures become a sea of grass. Inflorescence elongation seems to have a depressing effect on the non-flowering tillers of the same plant, for many of them die during this period. They give the appearance of having been deprived of water. It is obvious that death of some plants and shoots must occur in a stand of bluegrass each year in order to maintain an even density over the years. In ungrazed meadow grass the greatest number of these deaths occurs at this time of year. There is also a gradual dying of the leaves on the inflorescence itself, all but the upper one or two having turned yellow at the tip.

Beneath the soil new rhizomes are more abundant than ever. Some will turn up in the next few weeks; others may turn up sporadically throughout summer. All will turn up by early fall. It is a striking fact that new roots virtually cease to develop after April, though elongation of existing roots continues.

Rank growth in the unknown meadows of last year, especially the prominent white stems of last summer's purpletop (fig. 8), begins to blacken with mold, weaken and collapse. Lespedeza seedlings are coming up in patches of last year's crabgrass, and both orchard grass and wild barley are showing their flowering heads.

Cows drop their manure indiscriminately on the grazing places of horses, ignoring the careful system which the horses would maintain. Horses will avoid the grass around these cow-manure spots for a short time but in general the taboo against using grass around manure applies only within the species. In Germany, it was often the practice to apportion horses and cattle to pasture in such a ratio that rough areas were kept eaten clean, the horses cleaning up cow-dung patches, the cows the horse-dung grass. Cows are even now using some of the grass around piles of horse manure. Where horses graze with sheep, roughs are more evident (fig. 13); both species prefer the short grass, the sheep avoiding the grass around horse droppings almost as religiously as the horses themselves. Sheep drop most of their manure in loafing areas. What manure is dropped on the pasture is so easily scattered about that it seems to have very little residual effect. Grass fertilized

with sheep urine, however, has the same attraction as that fertilized by other stock.

During the last part of April when bluegrass leaves are soft and green, aphids are active, sucking juices from them. Very soon, however, lady-bug larvae begin reducing the aphid population, searching every blade its entire length for their green prey. In two weeks more these larvae will fatten and develop into full-fledged lady-bugs.

Now, in the last part of May, white clover (*Trifolium repens* L.) is flowering, and the inflorescences of Canada bluegrass are leaving the protection of surrounding leaves. Cheat (*Bromus* sp.) is ripening, yarrow (*Achillia Millefolium* L.) has begun to bloom, ironweed (*Veronia* sp.) is 18 inches high, and the first blades of purpletop are beginning to show. Kentucky bluegrass has mostly flowered and seeds are ripening. Steers have shifted from bluegrass to rosettes of redtop and are grazing them intensively. Since redtop blooms later than bluegrass it is still in an early stage of development, growing rapidly, and consequently more palatable and proportionately higher in protein and lower in fiber than the more mature plants of bluegrass. This is a demonstration of the general tendency of stock to seek during each part of the summer those plants which are immature. After redtop begins to flower, the leaves of pigeon-grass, purpletop and paspalum will be sought, and new lespedeza will be consumed eagerly. By the time these late-developing species have matured, cool-weather species such as bluegrass will have begun to develop palatable new fall growth.

It is interesting to see young rabbits cutting the tender flowering shoots of bluegrass that grow on rich creek-bank soil, then eating them, flowers and all. Occasionally they will prefer a dandelion stalk, which is consumed, stem, puff, and all.

Dung beetles are actively digging their tunnels into the soil, then excavating fresh manure which they carry down into their burrows. The soil brought up is spread out over the top of the cow dung, serving to keep the dung from drying out, inoculating it with a variety of soil organisms, and hastening the course of disintegration and the incorporation of this organic matter into the soil. Dung beetles play a significant part in maintaining the fertility of a heavily used pasture for they keep the cycle of fertility operating efficiently with little waste of time or material. Where pastures are lightly grazed, or merely mowed occasionally, there is not enough manure to maintain a dung beetle population, and manure that falls often remains undisturbed and undecayed for years. Under those conditions little if any fertility is restored to the soil by way of animal waste products. It is also significant that stock on rank pastures, where there is little clover or rich green grass, produce manure which is bulky, hard, and low in nitrogen. This has little attraction for dung beetles hunting a rich medium for their eggs to develop in. Manure of stock on rich pasture is loose and moist, and decays readily.

Machines which have been developed to cultivate intact sod by spiking or plugging the soil are following the precedent of the dung beetles, especially those devices which bring up small cores of soil and distribute them over the surface of

the grass. Much of the benefit of this machine comes from the loose soil which it adds to the surface of the ground and mixes with the litter of grass stems, encouraging their decay. In a small way, it simulates the natural process of flooding, whereby thin additions of alluvium from flooding streams are made to pastures on low ground.

Plots of grass experimentally burned in February are now decidedly more yellow-green than adjacent grass not burned. Inflorescences are less green and less full. Since the ground was moist and frozen when the plot was burned and the fire not at all hot, there was little if any consumption of decayed nitrogen-rich litter from the soil surface. The only loss was the overburden of summer leaves. The evidence of nitrogen deficiency in the plants and flowering shoots of the burned plot suggests that the tangle of leaves makes an important contribution to the nutrient economy of an ungrazed meadow.

A bluegrass pasture that is maintained by light grazing or mowing reaches a stability that is the result of a complex interrelationship of many factors. If we look down at it closely, it is a veritable jungle with many kinds of insects walking in and out among the fallen stems. There are worm castings, mouse droppings, white molds, and minute fungi. A few attenuated weed seedlings try to reach the light. Bluegrass roots come up during the summer into this community and feed, and they are as dependent on a balance of these organisms as they are on rain. As a matter of fact, in this litter moisture is retained, and the molds and fungi, thus encouraged to develop, release nutrients and build up important organic compounds. Prolonged mowing experiments which remove leaves to be dried and weighed for assays discourage this natural process and inevitably interfere with production. Many such tests, repeated year after year, report unexplainable declining yields as years go by. There is little doubt that destruction of the reigning balance of nutrient release inhibits forage production. Summer roots have no place to feed.

Disruption of the balance in a meadow sod by burning or continuous removal of clippings with consequent weakening of the cover encourages perennial summer grasses such as purpletop or broom-sedge which demand less nitrogen. With repeated burning it has been shown (Curtis & Partch, 1948) that fire can weaken bluegrass enough to allow prairie grasses and forbs to become established. This weakening involves, in all probability, the discouragement of tillering.

JUNE

In early June bluegrass inflorescences are still mostly rather greenish-yellow, though some patches tend to be more purple, or red. There is also much difference in the heights and leafiness of the flowering shoots. At first glance one might believe that the different patches are clones, displaying inherent differences but such is not always the case. Bluegrass is a very flexible plant, and it is subject to an unbelievable variety of influences and environments. Urine spots alone cause the development of many false clones, either by stimulating certain patches, or by

encouraging grazing in certain places. The differences between fertilized grass or grazed grass, and adjacent grass which has not been treated is often so striking as to seem uninterpretable except on a genetic basis. Time and degree of fertilizing influence the length and number of inflorescences and leaves. Close fall and winter grazing will produce plants with numerous small inflorescences and short leaves. Lack of fall grazing results in fewer and much longer flowering stems and longer leaves. Spots entirely avoided by stock for one reason or another will contrast with those which are grazed.

Treading also has its effect. Where pigs pastured intensively in winter, bluegrass is hardly flowering; the few inflorescences present are much shortened. The combined influence of actual killing of crowns by hooves, and the weakening effect of continual injury and nitrogenous fertilization played a part in preventing blooming. It was found, however, that hoeing of all top growth of grass from the frozen surface of the soil during February did not prevent crowns beneath the surface from sending up flowering shoots in spring, but it did greatly shorten the inflorescence, and weakened recovery growth. This weakness persisted throughout the summer, and the area was invaded by many plants, such as horseweed (*Erigeron canadensis* L.), milk purslane (*Euphorbia maculata* L.), *Paspalum pubescens* Muhl., boneset (*Eupatorium* sp.), purpletop, and white clover. Panicles on this plot ripened several weeks early, were abnormally white, and are already dropping seeds.

During this flowering season inflorescences are often found which have barely appeared out of retaining leaves and then died. The heads are a gray-white color, and the condition is often called silver-top. It is caused, in many cases, by the larvae of a thrip which consumes the soft tissue of the developing stem at one of the upper joints. This severs the panicle from its source of water and food and prevents its further development. While this thrip sometimes causes trouble for seed-raisers, the severance of the seed-head at this early stage undoubtedly conserves much vigor for the vegetative parts. Where silver top is common, the grass is commonly deeper green, but whether this is cause or effect is difficult to say.

Chicory is beginning to flower now. In Missouri this plant is an abundant weed along highways and in pastures. It does not become especially noticeable until June, spending both spring and fall as a prostrate rosette. Stock like to graze it in its immature stages, and to some extent even after its milky fruiting stems have begun to elongate. The seed of the plant is used as an ingredient of some pasture seed mixtures in England and has even occasionally been tried in this country. It has a long large tap-root which penetrates the soil deeply and thus serves some of the functions of sweet clover and alfalfa. Where pastures are not grazed in spring, chicory plants develop into tall bushy weeds full of pale blue flowers. Although adding a touch of beauty to a pasture, they become tough and inedible and leave their resistant stems to clutter up fall and winter grass.

In many cases where chicory has become objectionable, it is because the affected pasture was consistently not grazed in spring. If stock are allowed access to it at that time they will graze it closely and reduce its vigor. Fields along streams are

especially subject to chicory infestation for the simple reason that floods frequently break through fences during the spring season. Procrastination in repairing these fences often gives the chicory time to develop and seed, and build up reserves. Then when pastures elsewhere are grazed out, the fences are repaired and stock turned in on the low fields full of mature chicory. This gets rid of the overburden of summer grass, so that in fall when the chicory plant again assumes a rosette type of growth and begins to store up food supplies, it has full access to sun.

A single year's experiment to determine the effectiveness of spring grazing on restricting chicory growth was tried in some paddocks which had been ungrazed for some time and contained a heavy stand of chicory. Stock were allowed access to one paddock during April but were kept off the others till June. By July a strong reduction in height and vigor of the chicory stand was noted on the grazed paddock (fig. 18). The prominence of many weeds in certain fields can thus be traced back to the interrelationships of farm management and seasonal events.

By mid-June the tedious mowing of permanent pastures has begun (fig. 15). Although it is customary to wait until the seed head reaches its full growth before any mowing begins, it is quite probable that earlier clipping might be advisable so that the resources expended on production of the inedible mature panicle might be conserved for vegetative development. The observations already made of tillers dying during the period of elongation indicate that the plant is under stress at this time.

Earlier clipping would also prevent swaths from being so heavy. The bluegrass plant in the early flowering stage, when the panicle is just barely visible, is still fairly nitrogen-rich and soft and decays rapidly. As weeks pass, however, stems grow tough and siliceous, lie heavy on the new growth and disintegrate slowly. Even though the swaths are apparently obliterated in a couple of weeks by the rapidly growing June leaves, these leaves are forced to grow unnecessarily long through the weak light of the overburden and so deplete their food reserves. While it is essential to return this organic matter to the soil, it would be better to send it through the more efficient system, the animal, instead of trusting to the slow and expensive plan of decay. This is where the importance of grass silage comes in. Cut when grass is rich and generally in excess, and at the period when it is most beneficial to the plant, it is converted into manure and urine, rather than allowed to sink down slowly in an expensive disintegration. In well-grazed pastures there are now three main types of vegetation:

(1) There are those areas in present use for grazing which are short, rich, green and non-flowering. These places indicate where urine fell this winter and spring. They are full of clover, buckhorn plaintain (*Plantago lanceolata* L.), and chicory, all of which are being readily eaten. The rich nitrogenous grass is eaten closely.

(2) There are also those areas that were grazed last fall and winter, but are neglected for the time being. These show up now with short but well-developed inflorescences of bluegrass, mingled with chicory which has developed short flower-

ing shoots. Chickweed (*Stellaria media* (L.) Cyrillo) is common here, testifying to the fact that close fall grazing weakened the stand and exposed enough soil so that seed could germinate and the young seedlings receive sunlight all winter. Being winter annuals, they thrive best when winter competition is eliminated. *Paspalum pubescens* is also common in these places, since by the time fall and winter grazing occurs, this warm-weather species has already built up its reserves. Since fall-grazed bluegrass is slowed down in spring and its leaves shortened, the shoots of paspalum get off to a good start in May. Foxtail grass (*Setaria lutescens* (Weigel) Hubb.) is also beginning to become prominent in this short bluegrass.

(3) A third kind of area distinguishable on the pasture is the rough about manure, where tall chicory and rank bluegrass grow, and little if any grazing is taking place.

While these three conditions can be separately described as general tendencies where the pasture has been continuously grazed, they necessarily grade into each other to some extent.

Heavy rains after a dry spell freshen up the bluegrass rapidly. Much of this rapid greening-up results from rhizomes which, caught underground during the dry period, were unable to move. With the rains and resumption of rapid growth many of them come to the surface. Most striking response is that of the grass along shallow drainages in the pastures. Much of the reaction in this case is due not only to the availability of moisture, but to the concentration of the nutrients washed down or leached from the pasture hills above. In response to the accumulation of soil and nutrients in these shallow drains, they commonly support a vegetation distinct from that on adjacent slopes where removal of nutrient substances prevails. In one pasture, while the yellow soil of the slopes was thinly covered with a pure stand of Canada bluegrass the dark-soiled draws were distinctly marked off by tongues of Kentucky bluegrass. In another pasture, very poor and overgrazed, the hills were sparsely covered with triple-awn (*Aristida oligantha* Michx.), and lespedeza, with clumps of goldenrod (*Solidago altissima* L.) protecting a few remaining patches of old top-soil. In the gullies were chains of undernourished cocklebur.

Canada bluegrass is flowering now, and timothy heads are abundant in a few pastures and in the orchard. Redtop panicles are just now appearing. Ironweed flower buds are forming, lespedeza is coming up in pastures rooted by hogs this spring, and squirrel-tail grass (*Hordeum jubatum* L.) whitens the marshy swales in the hog pasture (fig. 16). This plant has the reputation of causing considerable difficulty with stock, especially when its heads find their way into hay. The bristles on the grain cause mouth injuries and open the way for more serious infection through diseases. Occasionally now small grasshoppers appear in the grass, and the first horseflies are giving the saddle-horses trouble. In a few parts of a Canada bluegrass pasture which I fenced off, rabbits have grazed the grass very closely. In these spots, opened up to the full strength of the sun, seedlings of buttonweed (*Diodia teres* Walt.) and also of sheep sorrel (*Rumex Acetosella* L.) come up, giving the appearance of small clones.

In a 15-acre pasture where a single horse had been grazing for 12 days I counted 18 newly burned urine spots on a plot 50 feet square. Since a horse averages around 7 urinations a day, in 12 days there would have been 84. If these urinations had been distributed evenly over the pasture there would have been only a third of a spot on 2500 square feet of the counted area. The concentration was actually 54 times that, indicating the extent to which grazing and urination are localized. The site of these counts was near the exclosure on the terrace in fig. 1. The soil was a rich fill and benefitted from subirrigation from the slope above.

Cattle, after having been turned into a pasture where pigs had run all winter, found many of the rank weeds to their liking. They ate avidly of the lamb's-quarters (*Chenopodium album* L.), tall smartweed (*Polygonum lapathifolium* L.), giant ragweed, and chicory (fig. 17). In a few days they had almost cleaned out even the Mexican tea (*Chenopodium ambrosioides* L.) and cockleburs (*Xanthium* sp.). They seemed to thrive on these weeds, even though the cockleburs are sometimes considered quite poisonous in their early stages of growth. About the only plants that the cattle could not stomach were common smartweed (*Polygonum Hydropiper* L.) and lady's-thumb (*Polygonum persicaria* L.). Consequently these two plants are taking over the old hog-feeding area. This indulgence in weeds took place at a time when plenty of good pasture was available.

JULY

The grass of pastures which have gone ungrazed is rank and lax, and is disregarded or trampled underfoot by stock. Where bluegrass has been kept short by continuous grazing, weedy annual grasses such as foxtail and crabgrass (*Digitaria sanguinalis* (L.) Scop.) come in. The former is especially common in closely grazed urine places, and actually contributes considerable forage. It is beginning to bloom, however, and that reduces its palatability. In the pastures not so closely grazed, stock are feeding on summer perennials such as purpletop and *Paspalum pubescens*, new shoots of sweet clover (*Melilotus* sp.), prickly lettuce (*Lactuca* sp.) and new lespedeza.

Pastures on low ground, partly as a result of extensive rains in June and July, are becoming much more rank and weedy than during previous drier summers. Bur marigold (*Bidens* sp.), *Croton capitatus* Michx., wild carrot (*Daucus Carota* L.), chicory, and *Paspalum pubescens* are coming up everywhere. When these weeds are cut during July mowing they leave a heavy swath which smothers out the grass and provides open areas where new weeds such as corn gromwell (*Lithospermum arvense* L.) can come in. At the same time, in an exclosure on this moist and rich low ground where no mowing at all went on last summer, much grass has drowned itself out, and weeds such as bull nettle (*Solanum carolinense* L.), black nightshade (*Solanum nigrum* L.), sedges (*Carex* and *Cyperus* sp.), and pokeweed (*Phytolacca americana* L.) are invading. The new poke plants are limited strictly to the vicinity of the fence, emphasizing that the chief means of

dispersal of poke seeds is by way of the alimentary tract of birds that eat the berries. Wherever convenient resting places such as fence rails, brush piles or fallen trees occur, there poke soon appears.

As these rank weeds develop in the grass, they shade it out. They are soon followed by giant ragweed and other rank bottomland vegetation, and eventually by elms and walnuts. On such rich wet ground removal of some of the rankness of the bluegrass is absolutely necessary for its own perpetuation. This can be most profitably accomplished by grazing, though careful late summer burning occasionally can be used. Mowing and raking is an expensive alternative. Upland bluegrass is much more stable and less subject to this self-destruction.

Although mowing in July is often done, it has little effect on pastures then except to shorten the grass for a time and postpone a little the flowering of certain prominent weeds. This postponement of flowering might help to reduce seed output were it followed later on with a second mowing. It often happens, however, that such mowings are never accomplished. Actually, many of these weeds are rhizomatous species, and occasional mowing seems to help more than hinder their spread. St. John's-wort (*Hypericum perforatum* L.) and chicory cut a few weeks ago already show flowers again. Ironweed (*Vernonia* sp.) comes back strong, and broad-leaved dock (*Rumex obtusifolius* L.) is scarcely affected.

When Canada bluegrass growing on exposed hills with little top soil is mowed, the hot summer sun has free access to the soil surface, which becomes dry and powdery. The slow process of restoring organic matter to these sterile places is consequently made even slower by indiscriminate mowing. Many farm practices such as manure spreading, fertilizing and liming, mowing and seeding, are done without reference to the natural conditions of the land. No effort is made to use ecological information to reduce the expense of wasteful blanket measures. Seed is not suited to the site, and treatment is not suited to the plant. The manure spreader is put into gear and manure flies over raw points and rich fills alike. As much seed is used on rich as on poor land. Alfalfa may be sown not only on suitable slopes, but on the poorly drained swales between. Mowing is performed when and where the opportunity offers without reference to the developmental stages of the plants or the nature of the soil. Heavy swaths smother bottomlands, and on thin soils the shrivelling litter offers no protection from sun and rain. To achieve maximum production and balance on an uneven farm, the ecological factors must enter into the picture.

Now that the spring drouth has been broken, rhizomes of bluegrass are elongating again. The drouth period is recorded on the rhizomes in the form of several extremely short joints, or internodes which contrast with the new ones nearly an inch long. While the axillary buds on these rhizomes seldom develop under ordinary sod conditions, this new flush of growth has resulted in considerable branching from the first one or two nodes of new growth. This branching seems to be a characteristic response of many plants to a break in drouth.

Gophers are throwing up mounds again. The fresh excavations are often disturbed and scattered by the mower bar during clipping of the pasture. They are also scattered by quail that use them for dusting places (fig. 21). These summer mounds usually develop a flora quite different from that of mounds pushed up in late fall. They are most commonly invaded by fleabane (*Erigeron annuus* (L.) Pers.), though also common are ironweed, boneset (*Eupatorium* sp.), thistle (*Cirsium lanceolatum* (L.) Hill), and other plants which germinate in summer, live for a fall and winter, and then flower the following summer. Old gopher diggings are often identified from a distance in summer pasture by patches of fleabane such as that shown in fig. 19.

Bare soil areas are also prominent where horses stand head to tail, brushing constantly at the horse-flies that are now abundant. The continual stamping of their feet digs up the soil over a considerable area. On windy days horses usually retreat to some exposed point high on a hill where their efforts are assisted by the wind.

In low shady places where the steer manure of last winter has remained moist, seed of honey-locust which passed through cattle undamaged have germinated, demonstrating one of the ways by which this plant spreads over pastures and waste land. Seeds of other plants also are able to navigate the alimentary canal of stock. From a small amount of hog manure planted in a flat with sterilized soil, bluegrass, nimble-Will (*Muhlenbergia Schreberi* Gmel.), goosegrass (*Eleusine indica* (L.) Gaertn.) and Mexican tea germinated (Etter, 1948).

August

Although August, like July, is usually a hot month, its days are noticably shorter, and it is perhaps this difference that makes bluegrass change for the better toward the end of the month. Often following a good soaking rain leaves seem to become a deeper color and broaden out slightly. Stock will leave their summer diet of purpletop, foxtail, lespedeza and weeds to graze the bluegrass where it has been kept short by summer traffic or close mowing, or where it has been grazed over by chickens for some time. A little anthocyanin may appear on the upper surface of leaves and on rhizome tips beginning to turn up. Some of the dormant summer buds on the crown of the plant have swollen. Most significant is the resumption of root initiation. As the month nears its end, short sprout-like rhizomes often develop, especially on meadow plants which have flowered. A rare plant or two, growing in a rich aerated nitrogenous soil, may even show the first development of a new tiller.

This new activity depends on the availability of moisture, and if August is very dry resumption of growth may be delayed, to occur in a flush of activity after the first rain. While no amount of water in July can make bluegrass really palatable or healthy, irrigation in August and September is a different matter. By allowing fall growth to get away to an early start while days are still warm enough to encourage growth, total forage can be much encouraged and its nutritional

quality will be reasonably satisfactory. Where bluegrass pastures are depended on to provide overwintering forage in the fields, dry falls can be very serious.

Other early signs that day length is getting short enough to produce results are the first fall flowering of dandelions and of annual bluegrass (*Poa annua* L.) and of the development from dry Canada bluegrass stems of new fall leaves which attract rabbits. The fall crop of grasshoppers also finds that this grass is beginning to have what they need to bring them to maturity, but many of them still prefer other more succulent sources of food. In lespedeza fields which were being saved for seed quite a few weeds were developing, especially prickly lettuce (*Lactuca scariola* L. and *L. saligna* L.). Grasshoppers invaded the field and while completely ignoring the lespedeza, they consumed leaves, seeds and stems of the weedy species, and almost entirely eliminated the weed problem before combining began. Grasshoppers are so uniformly castigated that it is interesting to observe also that they sometimes attack the giant ragweed with particular fury, consuming leaves and flowering heads before much pollen has had a chance to spill. Grasshoppers are often just as choosy as cattle or horses about which plants they eat. In a field of ironweed, a very troublesome plant, grasshoppers may strip certain plants completely, leaving only the bare stems. At the same time adjacent plants may be untouched. Ironweed is a highly variable species, and there are considerable differences in the leaf as to its hairiness, thickness, toughness, and greenness. There are probably equivalent differences in the chemistry of the tissues. It is small wonder that when they can afford it, the grasshoppers are particular.

August is a time of spider webs, and in the morning dew-wet webs may be seen scattered widely over the pastures. They are also abundant in the woodland, and can sometimes be seen flying overhead on the wind.

Mowing in mid or late August, while not a common practice, is very beneficial to pastures where summer grass has grown abundantly and deep. Mowing should be done just late enough to catch the last flowering shoots of the summer grasses such as purpletop, broom-sedge (*Andropogon virginicus* L.) crabgrass and foxtail so that no regrowth will occur. The removal of this overburden will permit the short fall blades of bluegrass to reap the benefit of all the fall sunlight which plays a big part in the amount of tillering that occurs as well as the width of leaves and the nutritiousness of the grass. This mowing should be done early enough, on the other hand, to allow considerable fall top growth to occur. In Missouri, the third week in August seems a good time. Later mowing will reduce the crop of grass which may be used for fall grazing or saved for winter subsistence.

September

The change which bluegrass began to feel in August has now brightened up the pastures except in ungrazed places where long summer leaves have begun to die and turn brown. Growth is rapid, summer rhizomes are turning up and leafing out, and in good soil a few plants may begin to form tillers. Just as in March, this September rebirth of activity results in a temporary absence of rhizomes.

Except for a few short sprouts in the meadow or on wounded plants, they are almost impossible to find. In good soil which has had plenty of air, water, and sun during August vigorous plants develop, and these often begin producing rhizomes in September and continue all fall.

This fall growth is at the expense of stored reserves, and the growth it produces is rather proteinaceous, though low in sugars. Summer rhizomes in the soil are depleted and weakened. Sods tend to fall apart rather easily as new roots develop. New leaves are definitely shorter and broader and stock show renewed interest in bluegrass. They may lose weight, or gain very little during this period as a result of the low sugar-high protein composition of the forage, and at the same time dairy cattle often show signs of acetonemia, or sugar shortage. As the days get shorter and the nights cooler, however, sugars will begin to accumulate and by November bluegrass will have a fairy high carbohydrate content provided the pasture has not been excessively grazed in fall. While work horses take readily to this new fall grass after being turned loose, they seem generally to prefer to consume considerable quantities of the more mature higher carbohydrate growth of nimble-Will and crabgrass before settling down to bluegrass and clover.

Winter annuals such as wild brome or cheat are now developing, just in time to replace the summer grasses such as purpletop, now flowering, and crabgrass and setaria, which are becoming rank or dying out. Cheat is now four to five inches high and furnishes good pasture. It is much sought after by stock and will continue to provide pasture until well into winter. It will also return early in spring to give stock an early bite. This is the wild counterpart of such crops as winter rye or wheat, often planted for late fall and spring grazing. As a matter of fact, while man has laboriously devised through trial and error pasture systems involving winter annuals and hot-weather annuals such as lespedeza or Sudan grass to supplement permanent grass, nature does it automatically on pastures, and stock take advantage of it instinctively.

On a hill which was seeded several years ago to lespedeza and timothy there is now a striking demonstration of the advantage of mowing at the correct time (fig. 22). Part of this field was mowed the latter part of June, while the timothy heads were still green and the stalks tender. The lespedeza seedlings were just getting a good start. The other part of the field was not mowed until more than a month later. The heavy strawy swaths can still be seen on this pasture. The lespedeza seedlings, shaded during their early development and then covered with grass, have scarcely produced any fall forage. Lespedeza in bluegrass also benefits by early mowing in late May or early June.

October

If the fall has been moist enough, October pastures may be as green as those of spring, but drouth in September and October, a frequent occurrence, cuts seriously into fall grass production. The greenest grass, as usual, is to be found in disturbed areas, where vehicles have passed, animals or men have walked, or chickens

scratched, in gardens or where new soil has been deposited either by flooding creeks or eroding rains. In these places fall bluegrass plants produce many rhizomes and tiller early and are sought by stock. If the plants have been extensively injured during late summer, however, as by burning, or by the cleats of farm machinery or by hooves of swine, the recovery growth may be very deep green and actively tillering, but very few if any rhizomes will develop. In general, such rhizomatous pasture or meadow species as quack grass, smooth brome, or redtop follow patterns of development similar to bluegrass, though slight differences in time of maturity are reflected in vegetative responses. None of these species is actively developing rhizomes now.

Hogs are feeding on bluegrass again, as they did during spring, testifying to the return of high protein forage. Cool weather and short days cause bluegrass to produce short leaves and prostrate plants. Stock graze closely seeking the nutritious foliage. They are invading grass protected during summer by rank foxtail or purpletop (fig. 23). Areas where urine fell last spring are still preferred, though little holdover effect is apparent. In pastures grazed during September spots of green grass are beginning to show where cattle urinated, but it is apparent that urine spilled in the hot weather of July and August produces virtually no results. The combined heat and dryness of summer permit the nitrogen to escape. Plots on which urine was applied artificially in August and September gave an amazing demonstration of the difference a month made (fig. 24). This fact has important meaning for grazers, for while it is commonly felt that animals return to the soil most of what they take from it, the truth is that much of the value of urine is lost when it goes on summer pastures. This might well influence the type of management which the farmer chooses to practice during that period, especially the dairy farmers who return the waste products of their cows to the fields during summer. It is quite possible that summer applications of manure lose so much nitrogen as to be unprofitable. Storage under protected conditions until cold weather might be more efficient.

Where pastures were not mowed in late summer the grass is very slow to develop and few if any tillers and rhizomes have formed. Fresh horse urine still kills the grass, but invasion of these burned spots is rapid now, at least in moist soil where adjacent plants have begun active rhizoming. Stock are avoiding the tall green grass around manure clumps.

The cessation of root initiation during summer causes an accumulation of buds without roots. During fall this backlog is reduced, and by October roots develop as soon as buds mature. These fall roots are fat and white and contrast with the slender wiry roots of summer.

There is now much mole activity, and gophers begin to build mounds out into closely grazed places seeking the succulent plants of dandelion and chicory. Clover is blooming a little, and aphids are back on the soft grass leaves. Under the oak trees where horses stand, fallen acorns are cracked beneath their hooves, and the soil becomes dry and powdery. Quail come to these trees, enjoy dust baths, and

pick up fragments from the cracked acorn shells. In the woods pasture they follow the hogs that crack hickory and walnuts and acorns with their teeth. Fragments dropped to the ground provide the quail with a convenient meal.

Bluegrass is often noticably superior under walnut trees. While this may be a complicated relationship involving microorganisms and obscure biochemistry, it also involves in part the fact that walnut leaves are shed early in fall, sometimes by mid-September, when bluegrass begins its important fall growing. Other trees often retain their leaves until November when all warm weather has passed. The shade cast in summer by walnuts is not dense enough to weaken growth, but is sufficient to limit rhizome development so that the grass does not become sod-bound. The sun of fall then allows tillering to progress and winter reserves to build up.

To test the influence of shade on bluegrass between September and November, a shade of muslin sack was placed a foot above the sod at the same time that walnut leaves were shed. This shade was left on until late-shedding trees such as maples had become bare. It had a noticeable effect on grass leaves, making them more lax, waxy yellowish green, and delayed the death or browning of summer leaves. In addition it was later noticed that the body of the fall leaves was much different. The shaded ones were fragile and shriveled and gray, while those in full sun retained their shape well and died to a tough yellow brown. The repercussions of this treatment were not followed the next year, but undoubtedly influenced the quality of recovery growth in spring, as well as the size and shape of the florescence.

November

In November bluegrass begins to suffer from the short days and the cold. Following the first frosts and the first freezes the blades shorten and cling to the ground. Rhizomes in vigorous grasses continue to be initiated, and to turn up, as they will, more slowly through the early winter. Nearly every new bud that develops now becomes a tiller. Gopher mounds are being invaded by rhizomes from adjacent plants. When the fall has been dry, stock begin to graze the rough areas where long grass remains. Clover leaves have been killed by the frost and swine are feeding on bluegrass, young chicory, and acorns. Canada bluegrass is just beginning to send out its rhizomes, which will continue growing off and on all winter and will turn up next spring to produce flowering shoots.

Pastures where sows and pigs were running during August were so softened by heavy rains that the unringed sows were able to attack the sod and uproot much of it in their search for worms, roots and other food. These rough bare areas still remain, testimony to the results of delaying too long ringing of the sows (fig. 25). In spring these rootings will be a maze of weeds.

December

Occasional frost has little effect on bluegrass, but in December when the soil freezes, bluegrass growth slows down greatly. With several inches of the top-soil frozen the leaves often turn dark, become flushed with anthocyanin. Wherever

bluegrass would like to grow but can't, as in frozen ground, dry ground, intense sunlight, or because of injury to growing leaves, it has a tendency to develop this purple coloring. Uprooted rhizomes become pink at the tips or occasionally for their full length. This is especially noticable in Johnson grass (*Sorghum halepense* (L.) Pers.) where the large fat rhizomes often turn a brilliant cerise when dug up and allowed to remain in the sun. Many other species seem to obey a similar compulsion.

Around manure clumps, the grass remains surprisingly green, and bluegrass rhizomes work beneath the clumps with indifference to the cold. The manure insulates the ground and prevents its freezing, thus allowing bluegrass to continue its growth and to build up its reserves. As a result of this advantage, the grass in these clumps gets away to an early start in spring.

Bluegrass leaves produced in December are very short, only an inch or two long. Except where the grass has been kept short, they are lost within the longer fall and summer leaves. When these old leaves die, pastures turn brown. In heavily pastured places, however, the grass is still green and stock still seek the sugar-rich grass. In many places, they are eating cheat seedlings in preference.

Gophers are very active, throwing up mounds overnight, especially in the longer grass areas where the soil is not so solidly frozen. Mice are once again building extensive tunnels in the sod, and when snow melts away, elaborate feeding runs bordered with cut leaves can be found in the shorter grass, ending here and there in large "haystacks" of reserve food.

Most fall rhizomes have turned up and now rest at the surface of the ground, though a few have been caught underground in the frozen soil. Tillering is still occurring, although the new shoots take several weeks to become large enough to be seen outside the retaining sheaths of their axillant leaf. Even more important than tillering, however, is the beginning of flower initiation. This process began on a few early plants last month, but is now general. A careful examination of the growing point shows a slight accumulation of extra plant segments at its tip, and it is from these that the panicle will develop. So it is that preparation for June pastures, full of waving bluegrass, is made even during this cold month half a year in advance.

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Explanation of Plate

PLATE 1

Fig. 1. January. On a pasture hill near the top, rooting hogs have defined the contact of a limestone and shale bed. Seepage along the contact favors their activity. Resulting changes in the vegetation will mark this contact for some time.

Fig. 2. January. Gilts in an orchard-grass pasture that was not mowed last summer beat paths among the resulting tussocks.

Fig. 3. February. During periods when snow and ice cover the ground horses feed on tall grass preserved in manured or weedy areas. There they can easily scrape the snow away with their hooves.

Fig. 4. February. Rank grass in orchards provides cover for cottontails. For sustenance, however, the rabbits prefer special spots where the grass is short and deep green. These spots usually show evidence of having received applications of urine. They are often grazed completely bare, roots, rhizomes and leaves all being consumed.

Fig. 5. March. Urine applied in a circle around this post in fall resulted in complete utilization of all grass, including subterranean parts, by mice. Even the post was eaten where urine had fallen on it.

Fig. 6. April. Old gopher mounds of last fall are partly covered with grass, but new ones remain barren and spring winds whiten them. These mounds, especially the spring diggings, provide opportunity for weed seeds to germinate, but also produce grass which is darker green, productive, and preferred by stock.

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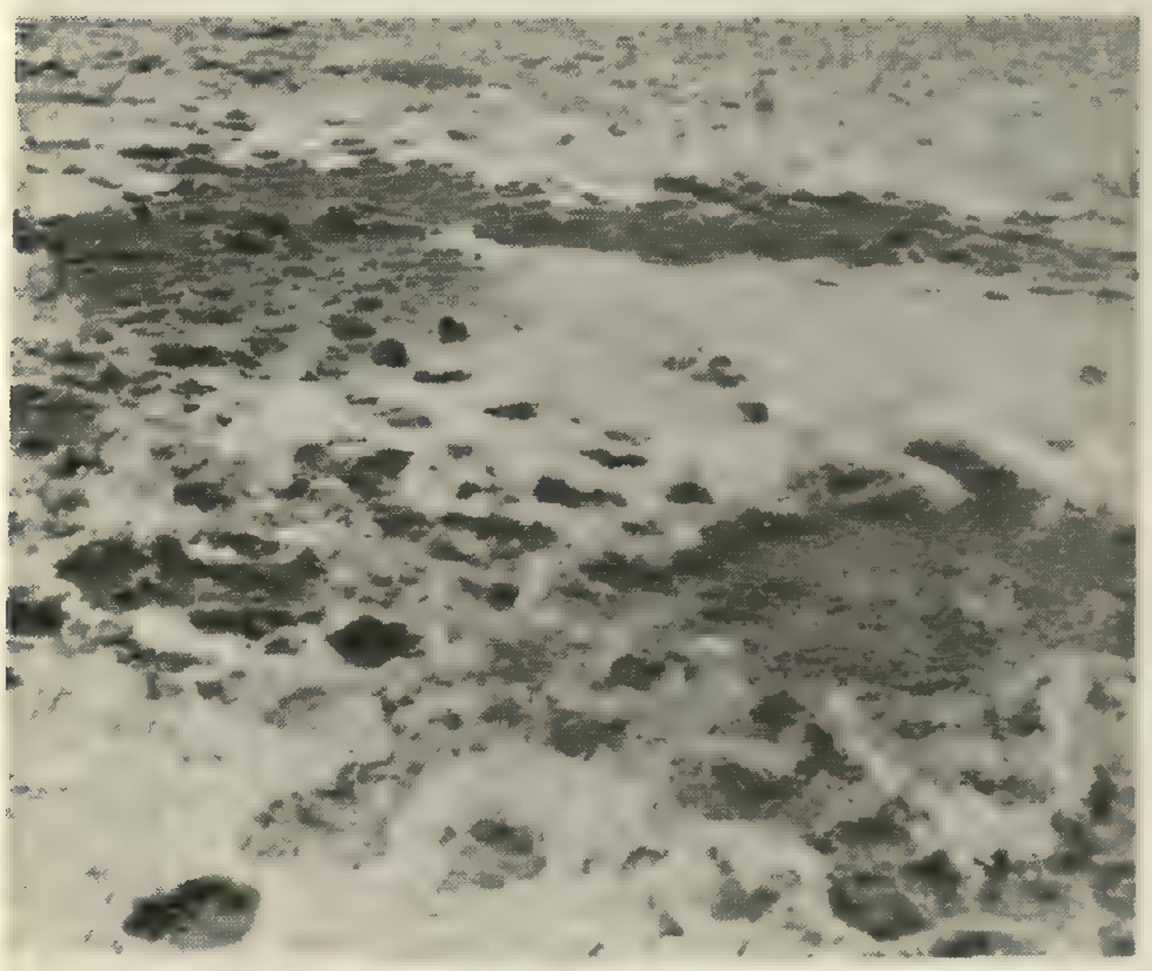

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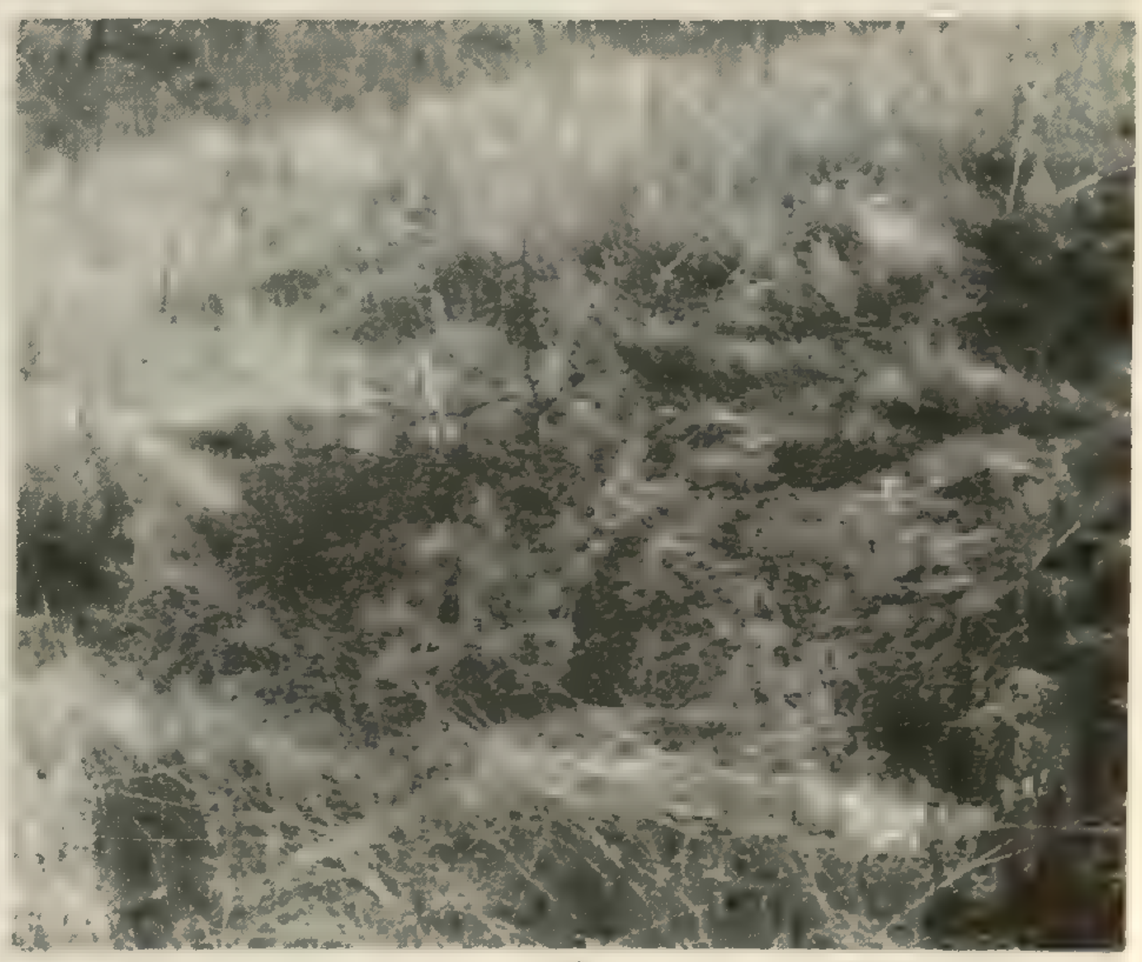

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EXPLANATION OF PLATE

PLATE 2

Fig. 7. March. At this time of year the pattern of horse grazing is very apparent. Rank grass remains uneaten while small areas are consistently grazed. These spots received continual applications of urine and remained green all winter.

Fig. 8. April. Stems of last summer's purpletop stand in the new rank grass of spring. When temperatures rise sufficiently to encourage molds and mildews, these stems will drop into the surrounding grass.

Fig. 9. April. Stock do not graze the rank grass round clumps of their own manure and rough areas thus appear in closely grazed pastures. Where cows and horses are grazed together these roughs are not so apparent since no prejudice seems to exist for grass contaminated by droppings of other animals.

Fig. 10. May. The spots of darker and taller grass in this picture received urinations from steers during fall and winter. The resulting grass growth is more nutritious and is preferred by stock. This pasture has not yet been grazed.

Fig. 11. June. When stock are turned in on a pasture such as that in fig. 10, they seek out the urine spots and consume the grass that grows there.

Fig. 12. June. Horses graze limited areas intensively. Under heavy grazing pressure these areas gradually expand. Urinations which burn the grass are concentrated near the periphery of grazings. The dead grass will be replaced by rich weeds and clover which will be grazed closely. Nutritious bluegrass will soon invade the spots and restore the turf.

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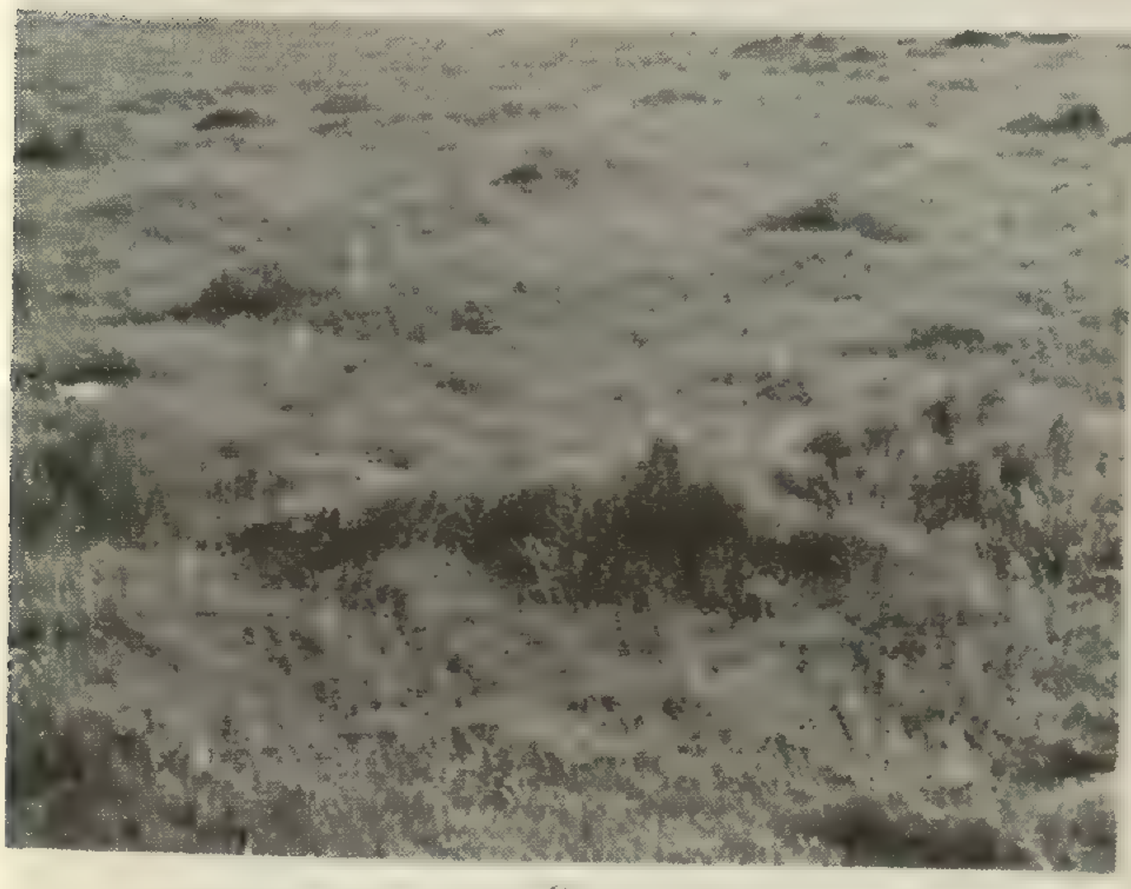

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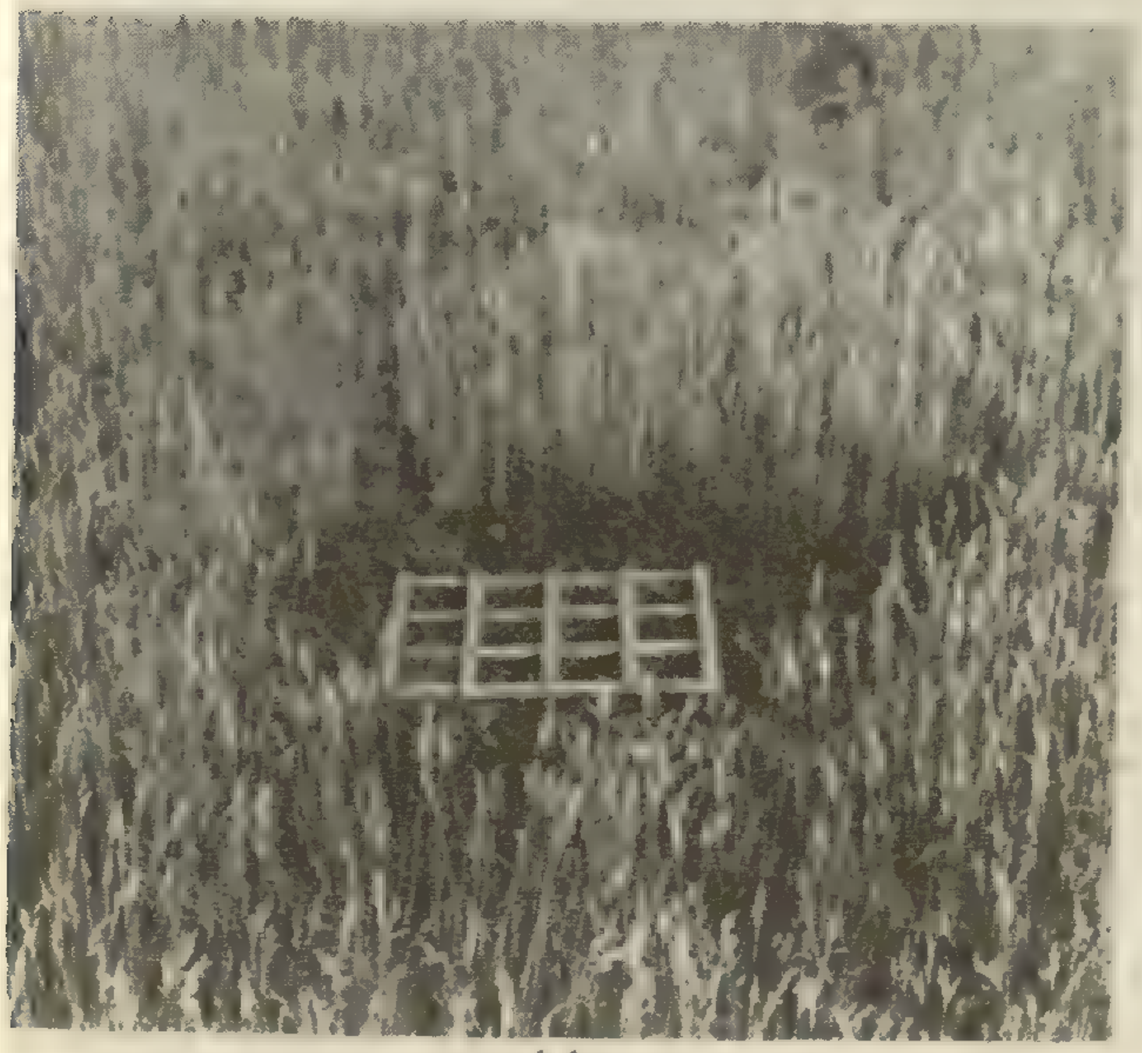

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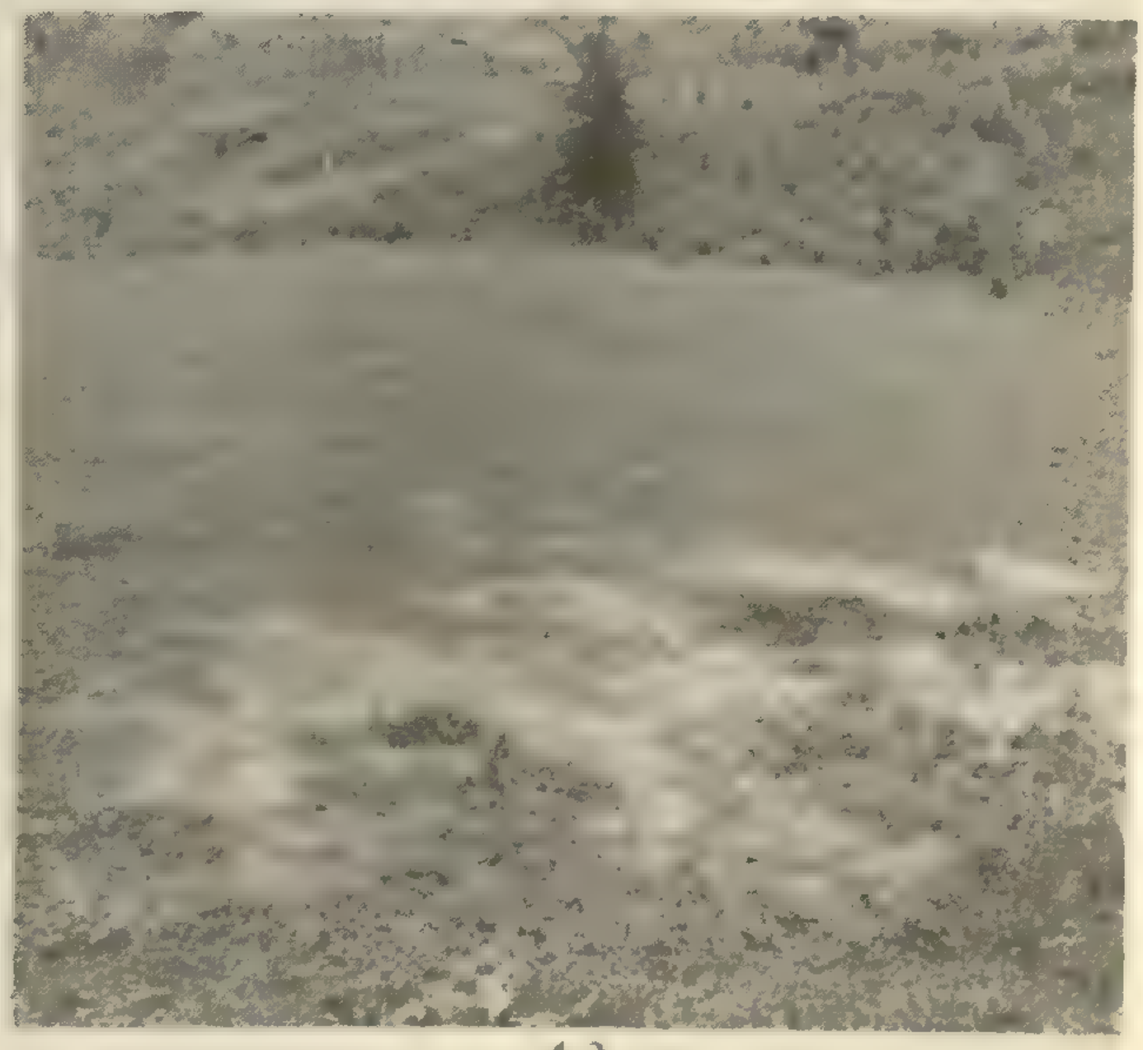

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ETTER—BLUEGRASS PASTURES

Explanation of Plate

PLATE 3

Fig. 13. June. When horse and sheep graze together stable rough areas are built up where horse manure accumulates. Sheep, like horses, prefer short grass. As grazing pressure increases rough areas are gradually whittled away.

Fig. 14. June. This illustration shows the effects of urine on the vegetation of a lawn. Not only does the grass thrive in the right-hand plot, but weeds are eliminated. Application here was about two-thirds gallon per square yard and was applied in June, the previous year, on moist soil.

Fig. 15. June. Mowing of bluegrass pastures commences. The heavy swaths will soon disappear beneath long summer leaves, but earlier mowing would have been desirable and would have maintained the food value of the grass at a higher level.

Fig. 16. June. In the swales of an old hog pasture squirrel-tail grass heads out. This grass often causes mouth injuries to stock that consume it in hay.

Fig. 17. June. Cattle turned into a new pasture in June sought first the rank growth of weeds that had grown up in areas where hogs had fed and urinated. The lamb's-quarters in the picture was cleaned out as were other weed species.

Fig. 18. June. Chicory is a bad pasture weed in some parts of Missouri. It can be controlled to a considerable extent by grazing it in spring since it is highly palatable then. Paddock in the rear was not grazed in spring at all while paddock in foreground was grazed during April. Grazing chicory while it is in the rosette stage weakens it and reduces the height of the coarse flowering stems.

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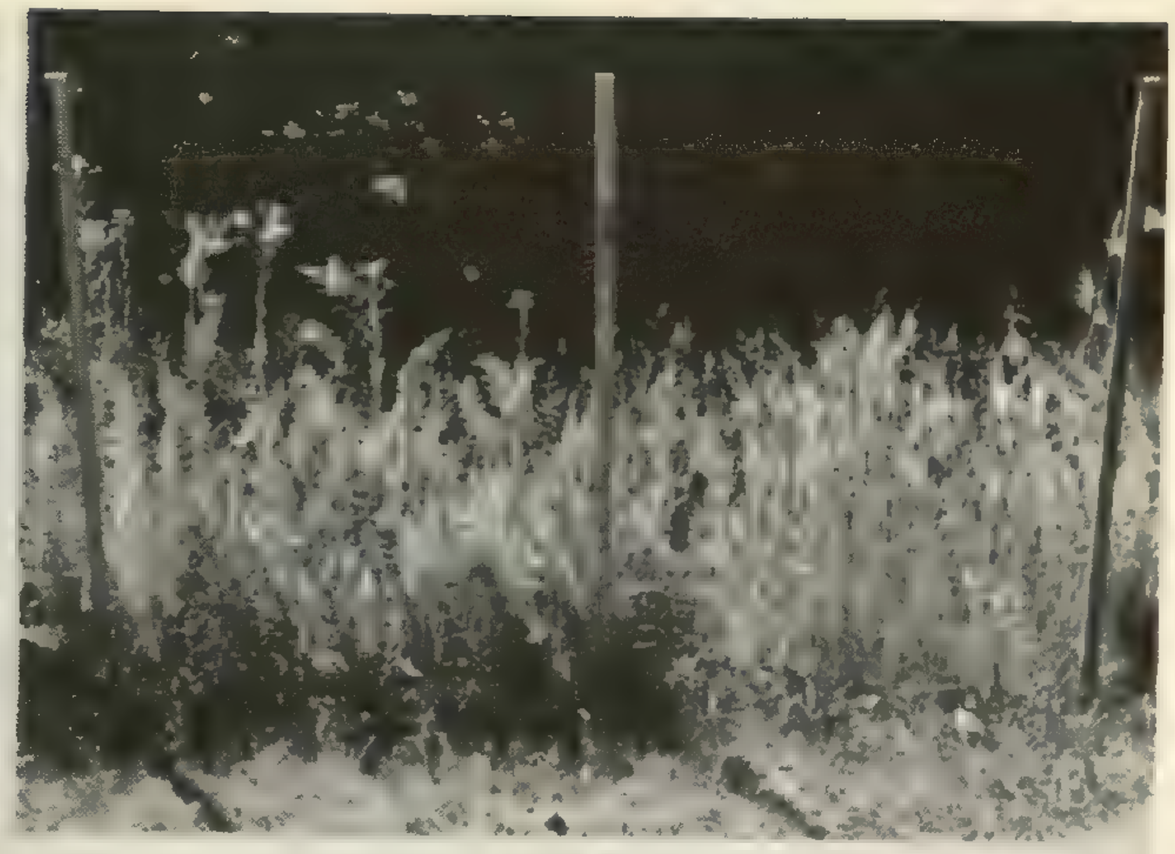

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Explanation of Plate

PLATE 4

Fig. 19. July. Gopher mounds in rank pastures are often indicated at a distance by a white growth of annual fleabane which germinates in the disturbed soil.

Fig. 20. August. Rabbits are choosey about where they graze. This small spot of crabgrass was grazed into the dirt. The grass was visibly darker green and had apparently benefitted from urine of some species.

Fig. 21. July. Quail use gopher mounds for dusting places.

Fig. 22. September. The time to mow is critical in pasture management and it varies with the species. In foreground a field of timothy and lespedeza was mowed while timothy heads were young and green. In distance where fall herbage is much inferior, mowing had been delayed till July.

Fig. 23. October. In late summer and fall foxtail grass comes into rich heavily grazed pastures. For a while it provides some good midsummer grazing, but, when seeding, is unpalatable. In fall, hungry stock invade the old foxtail and beat it to the ground.

Fig. 24. November. Urine has a striking effect on bluegrass noticeable in both fall and spring. In this picture, it is shown that this effect depends on time of application. Grass in the left plot was given urine in late August; on the right a similar application in late September. There was no visible effect from the earlier application.

Fig. 25. December. Late summer rains softened the soil and unringed sows up-rooted the turf. If this pasture were disced and harrowed slightly in early fall it would largely recover. If allowed to go into spring in this condition it will be covered with weeds.

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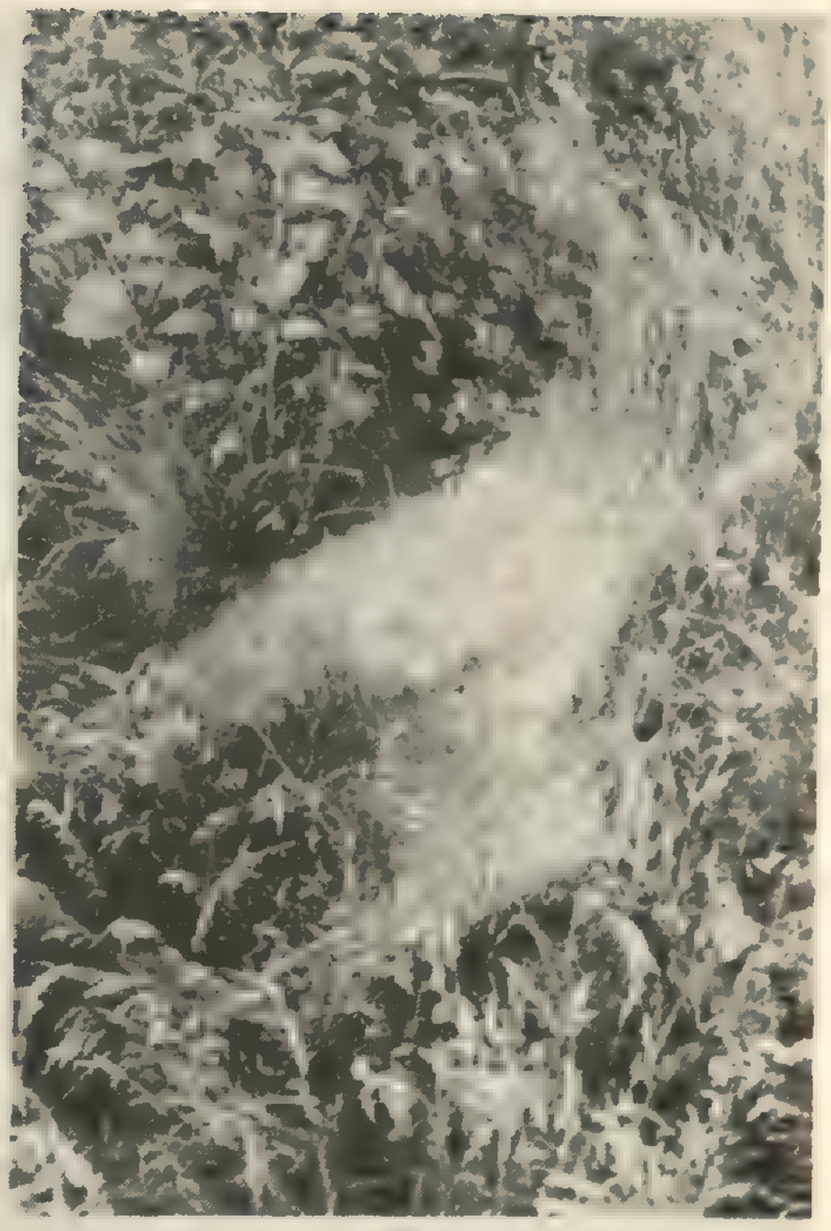

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THE POPCORNS OF TURKEY

EDGAR ANDERSON, *Missouri Botanical Garden*
AND
WILLIAM L. BROWN, *Pioneer Hi-Bred Corn Company*

The special significance of popcorns in the history of maize has been recognized by many students of that perennially fascinating problem (see, for instance, Sturtevant, 1894, Mangelsdorf, 1948). To scientists at large, however, the classification of popcorns and the description of the various ways in which they are used have been matters of such little moment that we were eventually driven to making our own world survey of popcorns and their uses (see Anderson and Cutler, 1950, for a general discussion). It was not until a decade of research had taught us to inquire in some of the most unlikely places that we learned (through Volney Jones) that popcorn is commonly used throughout Turkey and is a characteristic feature of many Turkish villages. At the very moment when we were endeavoring to have a comprehensive collection made for us there, Dr. Jack Harlan returned from that country with a collection of economic plants made for the Division of Plant Exploration and Introduction of the United States Department of Agriculture. Fifty-four collections of popcorn made by Dr. Harlan and his collaborators form the basis of the following report. We are indebted to Dr. Harlan for various observations supplementing the unusually complete data turned over to us by the Department of Agriculture, and to Dr. M. M. Hoover and his staff of the Regional Introduction Station at Ames, Iowa. It is a pleasure to acknowledge the efficiency and courtesy of this entire organization. We were welcomed to the increase plots in good weather and in bad, our attention was called to other collections of possible significance, and we were supplied promptly with viable seed of all the cultures we wanted to grow. For a few varieties of particular interest pertinent information was quickly produced from the files, and remnant seed of the original collections was made available to us.

The 54 Turkish popcorns collected by Dr. Harlan were grown in the experimental plots of the Pioneer Hi-Bred Corn Company at Johnston, Iowa, 20–30 plants being grown of each collection. A few varieties of particular interest were grown in replicate, and flint varieties and flint-dent mixtures from Dr. Harlan's collections were available for comparison in another plot. Each variety was scored for morphological uniformity, for season, for tassel type. Detailed measurements were taken on plant height, ear height, ear number, number of leaves above the ear, leaf length, leaf width, tassel exsertion, internode length and internode pattern, the width of the central spike of the tassel, glume length, the number of tertiary branches on the lowermost secondary branch of the tassel, the number of branchlets of the fourth order (if any), the number of secondary tassel branches, and the pubescence of the leaf sheath. At harvest time the plants were scored for husk number, for number of apparent nodes in the shank (the difference between these two numbers represents the number of condensed [telescoped] nodes of the

shank), shank length, shank width, kernel row number, kernel thickness, pith diameter, basal enlargement of the ear, pointing of the kernel, and color of pericarp and endosperm. At silking time regulation photographs of representative plants were made against a measured background. "Inclusive" herbarium specimens (Anderson, 1951) were made as a permanent record of each collection, each specimen including a photograph of the entire plant against a measured background and pressed central spikes and lower tassel branches.

Sporocytes of each culture were pickled in aceto-alcohol and smeared in the cytological laboratory. The number of chromosome knobs (a variable and diagnostic feature in maize—see, for instance, Mangelsdorf and Cameron, 1942) were determined and wherever possible knob positions were worked out. The results of these various measurements and scores are presented in Tables I and II. Photographs of representative plants are shown in pls. 5 and 6.

As soon as the collection began to tassel it was clear that maize is as heterogeneous a mixture in Turkey as are many other crops in that area (see Harlan, 1951). The variation within collections and between collections exceeded that in any of the collections of exotic maize from various parts of the world which we have had under observation. Three extreme types and three mixtures and intermediates between these extremes were apparent in the collection. One of these extremes was a popcorn identical with the variety known as Japanese Hull-less Popcorn. Since it came from Ankara, the capital city, and since most of the intermediates between it and the other two types came from the vicinity of Ankara or Istambul, the older capital, it probably represents a comparatively recent introduction into Turkey. It was strikingly different from the other two extremes. It had pubescent leaves, a heavy tassel with an extremely thick central spike, and the ear was elliptical in cross-section with a high number of rows of kernels, all of these features being characteristic of the variety Japanese Hull-less.

The other two extreme types were unlike popcorns commonly grown in the United States, and the two extremes, though connected by various intermediates, were quite unlike one another. One was very early to mature; the other was very late. The early type was short, with an exserted tassel, large glumes, and stiff upright tassel branches. Characteristically, the type had a low number of chromosome knobs, usually from none to three with either no knob on chromosome No. 6, or merely one small one. The late extreme was tall with numerous short internodes above the ear, which was borne high on the plant. The tassel was characterized by small glumes and lax branches, at maturity even the central spike remaining drooped over. The tassel was so included in the sheaths of the upper leaves that the lowest tassel branches were never completely free from the sheath of the uppermost leaf. Characteristically, it had seven to eight chromosome knobs, including two on chromosome No. 6 and one on No. 8. All these facts are set forth in the tables and the plates. Figures 1 and 2 show diagrammatically, but to scale, representative plants from the three most extreme collections of the two types.

The early extreme bears no close resemblance to any known race of maize though it is vaguely similar to several. It is rather like a somewhat degenerate form of the Northern Flint corns which were once characteristic of eastern North America. It is shorter and earlier than most of them, with somewhat smaller ears, higher row numbers on the average, and without the more or less enlarged base to the ear which is one of their most distinctive features.

The late extreme, on the other hand, belongs to a group of little-known popcorns with an intriguingly peculiar distribution. They are commonly grown by various aboriginal tribes along the borders of China and India; they were in early prehistoric times the prevailing type of maize on the coast of Peru and Chile; and they are still to be found here and there in various out-of-the-way places in South America. We received some years ago from Lorenzo Parodi, of Argentina, a popcorn of this general type and have a few scattered collections from Peru, Chile, and Colombia. Mangelsdorf and Oliver (1951) described and illustrated one from Caldas, Colombia. The collections from Turkey agreed with these Asiatic and South American popcorns in various technical characteristics of the inflorescence (see Alava, 1952)—in their knob numbers, the numerous ears high on the plant, the short upper internodes, and the drooping, included tassels. In its height, leaf shape, etc., the collection made by Harlan at Samsun was similar to varieties we have grown from the mountains of Siam, from the Naga tribes of Assam and from the Lushai Hills. Not only did it agree in general with these Oriental and ancient South American popcorns; with a popcorn collected in the mountains of Nepal (P.I. #166,162 called to our attention by Dr. Hoover), it was virtually identical. The collections from Nepal and from Turkey differed not as much as would two strains of any open-pollinated (i.e. non-hybrid) popcorn variety (such as Japanese Hull-less or South American) grown in the United States.

The three extreme types described above were apprehended by repeated study of the plants in the breeding plot. The exact association of characters was worked out more objectively by means of pictorialized scatter diagrams. One of these is presented in fig. 3. It has been set up to demonstrate the relationship for the seven characters which best differentiate the early flint-like popcorns from the late "Asiatic" extremes. As fig. 3 demonstrates, there is in the Turkish collections an over-all association for these seven characters, tassel exsertion, percentage of total height in the internodes above the ear, glume length, chromosome knob number, shank width, plant height, and ear height. At the upper right-hand corner of the diagram are the Asiatic extremes. As the diagram demonstrates, they are all plants with ears high on the plant, the internodes above the ears being proportionately short. They have narrow shanks, small glumes, and high knob numbers. At the lower left-hand corner of the diagram are the opposite extremes, a more variable lot. They tend to be short, low-eared plants, with exserted tassels and proportionately long internodes below the tassel. They have wide shanks, long glumes, and few or no knobs on their chromosomes. It will be seen that though the Asiatic extremes seem to be somewhat set off from the rest there is a gradual

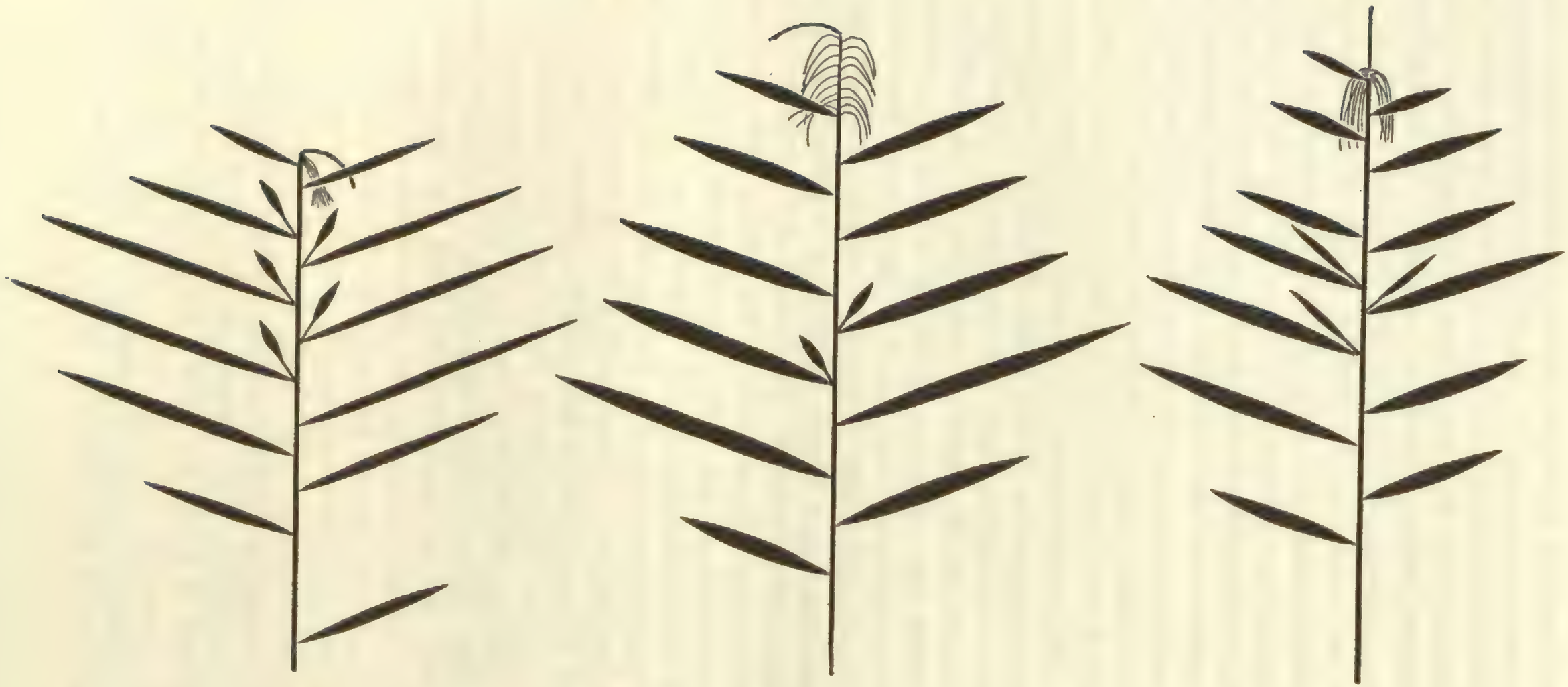

Fig. 1

Three examples of the "Asiatic" race of popcorn, highly diagrammatic but exactly to scale (× 1/25). The lengths of the internodes, of the leaves, of the shanks, and of the branches of the tassel are all to scale, and the shape of the tassel is copied from photographs of fully mature tassels. Each diagram represents a different collection. Note the short internodes, the drooping included tassels, and the multiple ears high on the plant.

Fig. 2

Three examples of the "Aegean" race of popcorn, to the same scale and prepared in the same way as fig. 1. Note the exserted tassels, the longer internodes at the upper part of the plant, and the low ears.

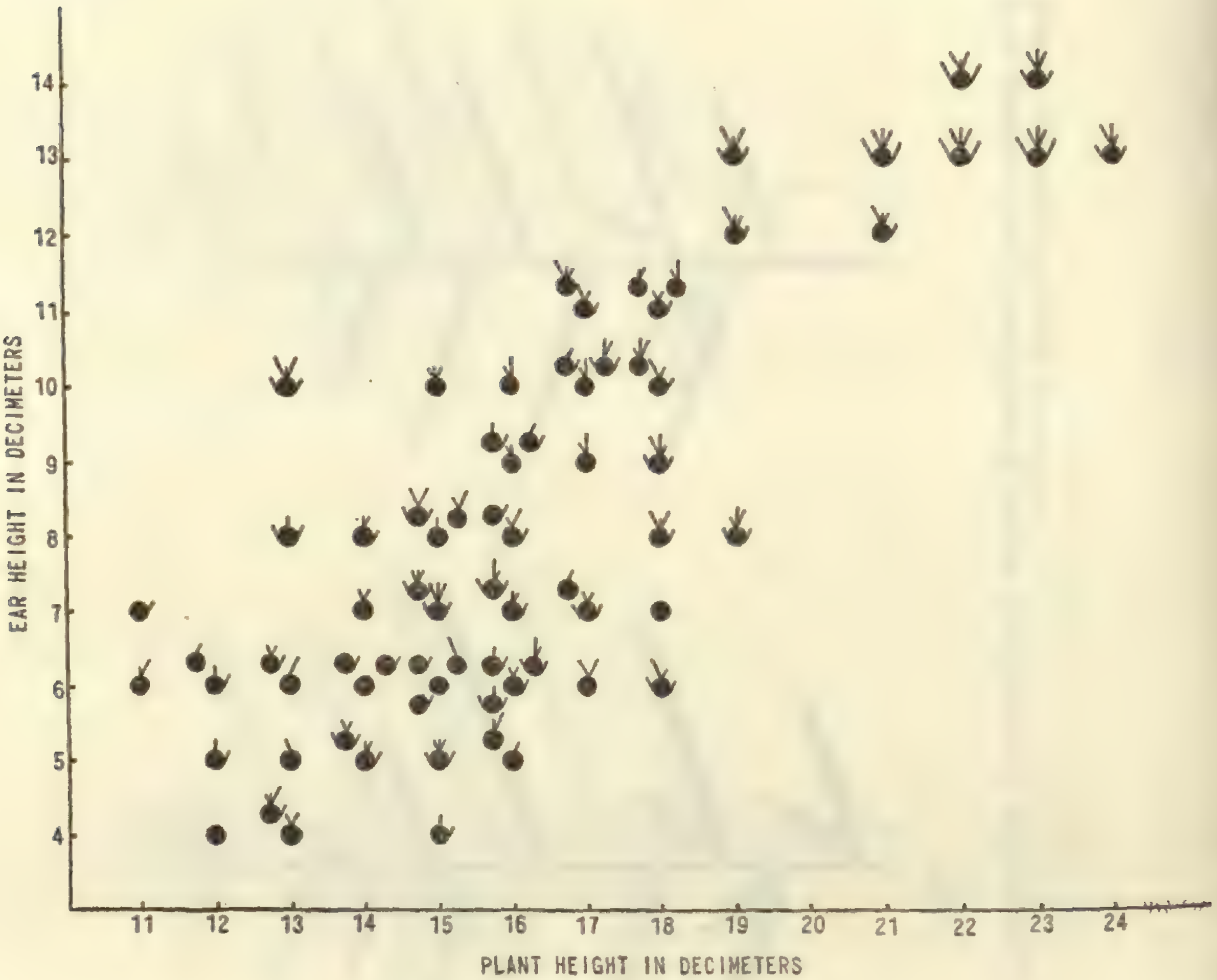

Fig. 3. Pictorialized scatter diagram illustrating the variation in Harlan's collection of Turkish popcorns for seven characters. Each dot is a diagram of a single plant for each collection, the plant having been chosen in the field as most representative for that particular collection. Further explanation in the text.

transition from one extreme to the other. The diagram presents an exact picture of the way in which two diverse races of maize have been brought together and have intermingled, forming a variable set of intermediates. Some of these are extreme recombinations in which characters of one race have been combined with characters from the other. For the whole group of varieties, however, there can be demonstrated the continuing association, *on the average*, of those characters which went in together. For those not familiar with the recent work on races of maize it should be pointed out that just such a mingling of correlated variables is characteristic of maize. It has been shown for Mexico by Wellhausen, Roberts, and Hernandez in collaboration with Mangelsdorf (1951, 1952), who have greatly extended the preliminary studies of Anderson and Cutler (1942) and Anderson (1946). For the maize of the American corn belt where purposeful mixing of two races has been carried on intensively, Brown and Anderson (1947) were able through these correlations to work out the history of the mingling by these indirect methods before carrying on the historical and archaeological research which proved that it had indeed occurred in just such a way (Anderson and Brown, 1952). There can be little doubt then that the heterogeneous popcorns of Turkey were largely derived from the mingling of popcorns from the two widely different races of maize, the resulting mixture being made somewhat more diverse by the comparatively recent addition of still other types of popcorn.

After the racial affiliations of the 54 collections made by Dr. Harlan had been worked out, their distribution in Turkey was determined from his collecting notes. The resulting picture is a simple one. The Asiatic race in its purest form is characteristic of the mountainous areas in northeastern Turkey. The other race is characteristic of the Aegean shores of Anatolia and we are accordingly referring to it as the Aegean race. It is possible to turn the pictorialized scatter diagram of fig. 3 into a crude sort of index running from 0 to 14. By plotting these index numbers in four grades it is possible to demonstrate the mingling of the Aegean and Asiatic races of popcorn as reflected by Dr. Harlan's collections (fig. 4).

Conclusions:

From the evidence presented above we conclude that popcorn is widespread in Turkey. Though heterogeneous there even for maize, it can be assigned to two provisional races, the Aegean and the Asiatic. The former is commonest along the coast, the latter in the northeastern mountains. Most of the popcorns of Turkey are various intermediates between these two extremes, occasionally modified by more recent introductions of modern commercial varieties.

In the above report there is little or no evidence to indicate when or where or by whom these popcorns were introduced into Turkey. To answer such questions we have begun a series of ethnological, linguistic, and historical inquiries. These investigations have proceeded to the point where we are confident that though the problem is a complex one, it is not chaotic. It seems probable to us, in the

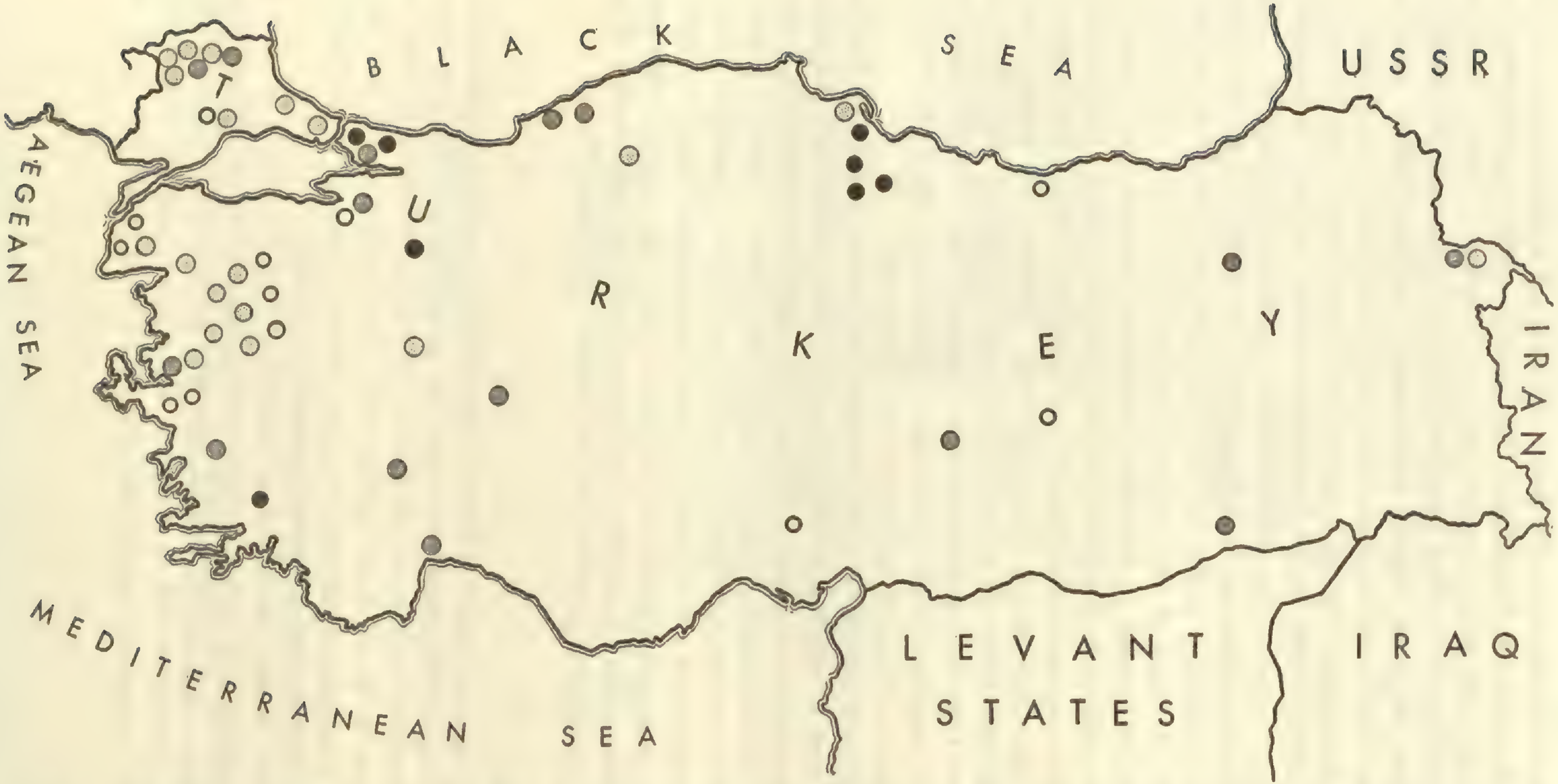

Fig. 4. Distribution of the original collections made by Dr. Harlan and diagrammed in fig. 3. The numerous collections in and around Ankara, the capitol city, have been omitted. The values of fig. 3 have been turned into a crude index running from 0 for typical "Aegean" varieties to 14 for typical "Asiatic" varieties. Solid black dots represent collections most like the Asiatic extreme (those in the upper right-hand corner of fig. 3); open circles, the most extreme Aegean types; lightly stippled dots, intermediates resembling Aegean; heavily stippled dots, intermediates resembling Asiatic race.

light of all the evidence, that the Asiatic and the Aegean popcorns were brought to Turkey at different times, and by different routes. Further discussion must be postponed until other evidence can be presented.

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TABLE I

Turkish popcorns listed in the order of their official plant introduction numbers. For each collection there is given the place where the seed was collected, the season of maturity, the variability of the plants grown from that collection, the height of the plant in decimeters, the height of the uppermost ear in decimeters, the number of ears, the length of the uppermost internode in centimeters, the length of the male glume in millimeters and the Index number on a seven-fold index with values of 0 for extreme "Aegean" types and of 14 for extreme "Asiatic" types (further explanation in the text).

Plant Introduction Number	Place	Season	Variability	Height of plant in dm.	Height of ear in dm.	Number of ears	Length of uppermost internode in dm.	Length of glume in mm.	Index Number
164,994	Cayirhan, Ankara	Mid	Uniform	14	8	2	2.3	10	3
165,036	Nallihan, Ankara	Mid	Uniform	15	8	2	2.4	10	1
165,057	Beypazare, Ankara	Mid	Variable	16	9	2	1.8	11	1
167,030	Kirik-Khan, Hatay	Late	Variable	18	11	2	2.2	12	5
167,947	Kulak, Balikesir	Mid	Uniform	15	5	3	1.9	10	5
167,948	Bursa	Early	Uniform	15	6	2	2.7	12	0
167,949	Balikesir	Early	—	16	6	2	1.9	13	3
167,963	Bucak, Burdur	Late	Uniform	18	9	2	1.8	8	8
167,967	Osman Buku, Aydin	Mid	Uniform	15	7	2	1.7	9	8
167,983	Koycegiz, Mugla	Very Late	Uniform	23	15	2	1.6	9	12
167,989	Akhisar, Manisa	Mid	—	16	9	2	2.2	9	2
168,000	Istanbul	Mid	Uniform	16	8	2	2.1	9	4
168,006	Kirklareli	Mid	Uniform	15	10	2	2.0	10	4
168,007	Kirklareli	Mid	Uniform	16	10	1	2.1	9	4
168,008	Kirklareli	Mid	Uniform	18	11	2	2.1	9	5
168,016	Tekirdag	Mid	Uniform	15	6	2	2.4	10	1
168,017	Tekirdag	Mid	Uniform	15	4	2	2.2	10	2
168,019	From a seed store	Early	—	16	9	1	2.3	10	2
168,027	Ayvacik, Canakkale	Early	—	14	6	2	2.1	12	0
168,032	Edremit	Mid	—	16	6	2	2.4	9	2
168,033	Balikesir	Early	Uniform	12	5	2	2.1	10	2
168,039	Kulak, Balikesir	Early	Uniform	15	6	1	1.3	11	2
170,877	Manisa	Mid	Uniform	14	6	2	2.5	11	1
170,879	Soma, Manisa	Early	Uniform	13	4	1	2.1	12	2
170,880	Istanbul	Mid	—	13	6	2	2.7	12	2
170,881	Cayirova, Kocaeli	Mid	Uniform	18	10	3	1.6	11	6
171,896	Inceoglu, Bartin	Late	—	13	10	3	1.4	10	8
171,912	Tokat	Very Late	Uniform	22	13	3	2.5	9	14
171,915	Niksar, Tokat	Very Late	Uniform	23	13	3	1.2	8	14
171,917	Niksar, Tokat	Very Late	Uniform	22	15	3	1.0	10	13
172,600	Igdir, Karahisar	Mid	—	13	8	2	2.0	10	3
173,830	Malatya	Mid	Uniform	14	6	2	2.2	11	1
174,414	Mardin	Late	Uniform	17	11	2	1.7	11	6

175,976	Biga, Canakkale	Early (Mid)	—	11	7	2	2.2	13	1
175,978	Biga, Canakkale	Early (Mid)	—	13	4	2	1.8	10	5
176,801	Erzincan	Mid (Late)	—	15	7	2	1.7	10	5
176,804	Ayfon, Karahisar	Late		17	6	2	1.5	12	5
177,114	Araplar, Ayvalik, Balikesir	Early	Uniform	11	6	2	2.0	10	3
177,583	Ankara	Late	Uniform	15	8	2	2.2	11	6
177,598	Ankara	Early	—	12	6	2	2.0	11	2
177,622	Ankara	Mid	—	15	8	2	2.0	9	3
177,624	Ankara	Mid	—	18	8	2	1.5	10	7
177,625	Ankara	Early	—	16	5	1	2.8	11	1
177,626	Ankara	Late	Uniform	15	5	1	2.0	10	—
177,628	Ankara	Late	—	17	7	1	2.3	12	5
177,631	Ankara	Mid	—	16	6	1	2.1	10	3
177,637	Ankara	Late	—	16	7	2	2.5	10	3
177,641	Ankara	Mid	—	16	7	2	2.8	11	5
177,643	Ankara	Mid	—	18	7	2	2.8	12	1
179,127	Kalecik, Ankara	Mid	—	16	5	2	2.7	10	3
179,131	Alpagut, Sakarya Eskisehir	Late	—	19	13	3	1.9	10	11
179,566	Altinova, Ayvalik, Balikesir	Early	Uniform	12	6	2	1.8	10	1
179,568	Araplar	Early	Uniform	13	5	2	1.7	11	1
179,579	Sehir, Sebin Karahisar, Giresun	Mid	—	13	7	2	1.6	12	—
182,324	Bolce Agac, Manyas, Balikesir	Early	Variable	12	4	2	1.8	11	0
182,326	Elbistan–N.E. of Tarsus	Mid	—	19	8	1	2.2	9	9
182,327	Igdir, Karahisar	Mid	—	17	11	1	1.3	10	6
182,785	Gemlik, Barsa	Mid	—	18	10	2	1.4	9	7
183,750	Karga ili, Kastanou	Mid	Uniform	18	11	2	1.8	10	4
183,751	Karet-Satranbolu, Zonguldak	Late	—	24	13	2	1.8	9	11
183,756	Kozam, Adana	Mid	—	15	6	2	2.9	11	1
183,764	Kilic, Kesan, Edirne	Early	—	14	7	2	2.0	11	2
183,771	Edirne	Mid	—	14	5	1	2.3	10	3
183,783	Lalapasa, Edirne	Early	Variable	14	5	2	1.9	12	4
183,787	Ankara (near)	Mid	—	18	6	1	1.9	12	6
183,790	Manisa	Mid	—	16	6	2	2.4	11	5
183,798	———	Mid	Variable	16	8	1	2.8	11	1
185,045	Elmali, Antalya	Late	—	17	10	2	2.5	9	4
185,063	Bafra, Samsun	Mid	—	13	6	2	1.7	11	3
185,073	Akesehir, Kohya	Late	—	16	9	2	1.9	11	5
167,030	Misifite	Late	—	17	9	2	2.1	9	4
167,030	Misifite, from farmers at Kirik-Khan, Hatay	Late	Variable	17	10	2	1.7	8	8
170,881	Cayirova, Kocaeli	Late	—	19	12	2	1.4	10	9
170,881	Cayirova, Kocaeli	Late	—	21	12	3	1.1	10	9
171,904	Seed dealer in Samsun	Very Late	Uniform	19	12	3	—	10	14

TABLE II

Numbers and positions of chromosome knobs for the collection of popcorns from Turkey. The numbers at the left are the official plant introduction numbers of the Bureau of Plant Exploration and Introduction. Numbers 1 to 10 in the heading at the right refer to the 10 chromosomes of *Zea Mays* as recognized by maize cyto-geneticists. The final column, "B", records the numbers of "B" chromosomes, if any. Where no number is given, there were no "B" chromosomes. —1 indicates a knob on either one of two chromosomes. "s" = small. "T" = terminal.

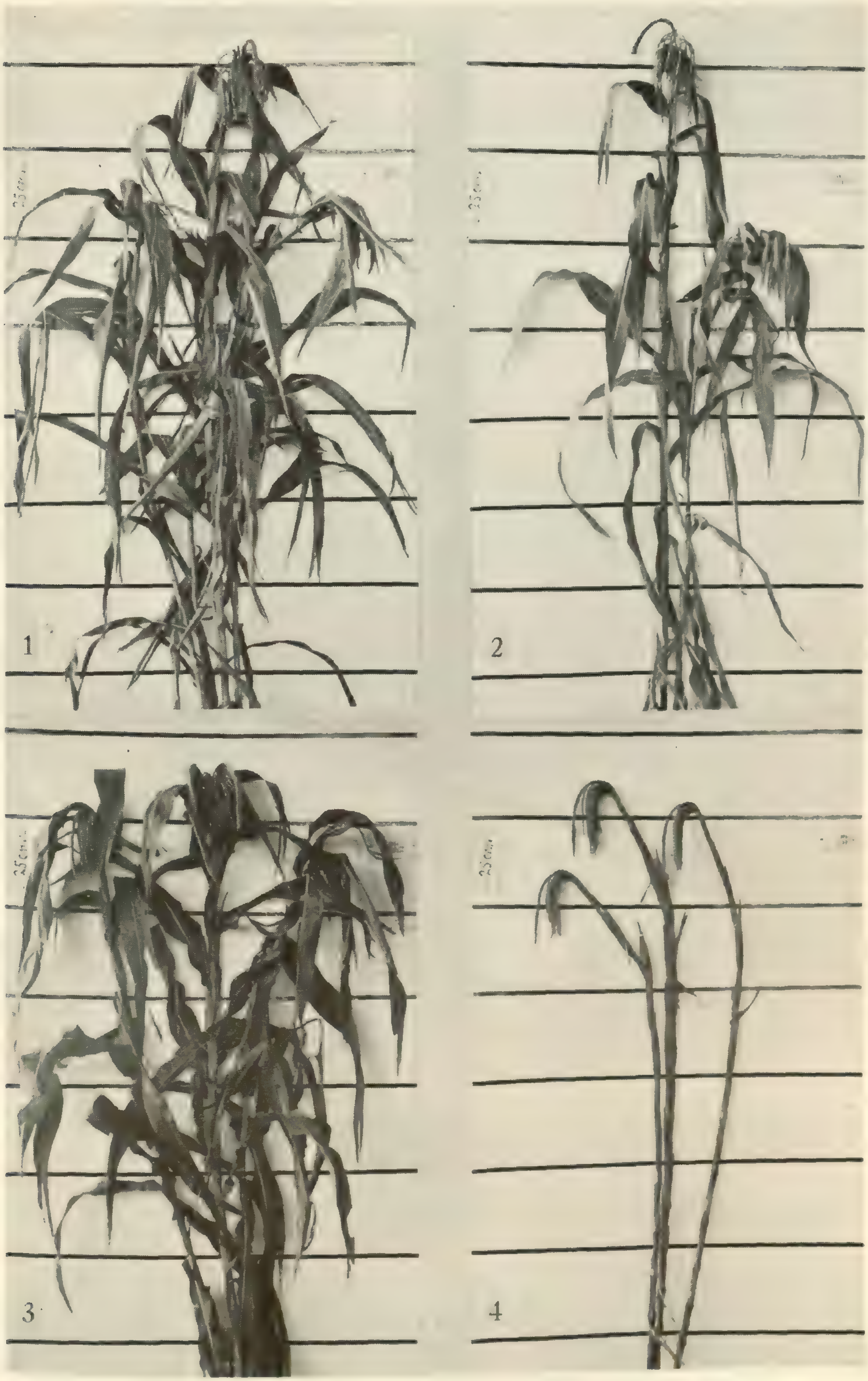
Number	Number of knobs	Knob position										
		1	2	3	4	5	6	7	8	9	10	B
P. I. 164994	4						2	—1	—	1T		
P. I. 165036	1						1					
P. I. 165057	4						1	1	1	1T		
P. I. 167030	4				1		1	1		1T		
P. I. 167947	5		1				2	1		1T		
P. I. 167948	2						0	1	1	0	0	
P. I. 167949	3						0	1		1T		
P. I. 167963	6		1		1?		2	1	1			
P. I. 167967	5	0	1	1	1	1	0	—1	—			
P. I. 167983	6–7						2	1	1	1T		
P. I. 167989	2						0		1	0	0	
P. I. 168000	4		1				0	—1	—	1T		
P. I. 168006	1				1		0					
P. I. 168007	2					1?		1				
P. I. 168008	3						0		1	1T		
P. I. 168016	3						1	1		1T		
P. I. 168017	4			1			1	1		1T		
P. I. 168019	3						1	1		1T		
P. I. 168027	1						1					
P. I. 168032	3						1	1	0	1T	0	
P. I. 168033	2					1	0	1				
P. I. 168039	0											
P. I. 170877	3						1		1	1T		
P. I. 170879	1						0			1T		
P. I. 170880	3		1				0	1	1			
P. I. 170881	4						2	1	1			
P. I. 171896	5	1s	1?				2			1T		2
P. I. 171912	8	0		1	0	1?	2	1	1	2	0	
P. I. 171915	7–8	1s					2	1	1			
P. I. 171917	7?						2	1	1	1T	0	
P. I. 172600	6	1s					1	1	2	1T	0	
P. I. 173830	3	0	1s				0		1	1T	0	
P. I. 174414	3		1		1		0	1	0	0	0	
P. I. 175976	4		1				1	1		1T		
P. I. 175978	3						1	1		1T	0	
P. I. 176801	6		1				2	1	1	1T		
P. I. 176804	1				1		0					
P. I. 177114	2					1?				1T		
P. I. 177583	5	1?					2	1	0	1T	0	
P. I. 177598	3					1	0	1		1T	0	
P. I. 177622	2							1		1T		
P. I. 177624	4						1	0	1	1T	0	
P. I. 177625	2	0	1s				0		1	0	0	
P. I. 177626	2			1?			0	1				
P. I. 177628	6	0	1	0	1	1	2	1?		0	0	
P. I. 177631	5		1		1		2	1				
P. I. 177637	3		1		1		0	1		0	0	
P. I. 177641	5						1	1	2	0	0	
P. I. 177643	2						1	0	1	0	0	
P. I. 179127	1									1T		
P. I. 179131	5		1		1		0		1	1T		

Number	Number of knobs	Knob position										
		1	2	3	4	5	6	7	8	9	10	B
P. I. 179566	2					1	0			1T	0	
P. I. 179568	2							2				
P. I. 182324	2						0	1		1T	0	
P. I. 182326	4						1	1	2			
P. I. 182327	2						0	1		1T		
P. I. 182785	1		—1	—								
P. I. 183750	4			1?						1T		
P. I. 183751	5?									1T		
P. I. 183756	4						2	1		1T		
P. I. 183764	1							1				
P. I. 183771	3						0		2	1T	0	
P. I. 183783	5			1		1	0	0	2	1T	0	
P. I. 183787	5						2					
P. I. 183790	5					1	0	1	1	2	0	
P. I. 183798	4		1	1			1		1			1
P. I. 185045	3						1			1T		
P. I. 185063	3L						1	1		1T		
P. I. 185073	2?							1		1T		
P. I. 167030	2									1T		
P. I. 167030	5L						2	1	1	1T	0	
P. I. 170881	3L						1	1	1			
P. I. 170881	3						1	1	1			
P. I. 171904	8			1	1	1	2	0	1	2	0	

Explanation of Plate

PLATE 5

Four plants of Dr. Harlan's collection from Samsun, Turkey, photographed against a measured background, at the time when the tassels were actively shedding pollen. Note the drooping tassels, barely exserted from the upper leaves, the ears high on the plant. Specimen No. 4 has had its leaf blades and most of its leaf sheaths removed. The lines in the background are 25 cm. apart.



ANDERSON AND BROWN—TURKISH POPCORNS

Explanation of Plate

PLATE 6

The same "Asiatic" popcorn of pl. 5, photographed in the field at harvest time.

Fig. 1. Plants photographed in the experimental plot. Note the ears high on the plant, the drooping tassels, and the plant-to-plant uniformity. These plants were grown from remnant seed actually collected in Turkey. The uniformity of this variety is characteristic of collections made both in Nepal and in Turkey.

Fig. 2. Three plants from the same row as those in fig. 1, laid down on the earth of the breeding plot. Note the multiple ears, high on the plant, the leaves continuing to the very base of the tassel, the drooping tassel branches, the slender stem, and the short silks. These are all characteristic of Asiatic popcorns.

ANDERSON AND BROWN—TURKISH POPCORNS

A PRELIMINARY SURVEY OF THE MILPA SYSTEM OF MAIZE CULTURE AS PRACTICED BY THE MAYA INDIANS OF THE NORTHERN PART OF THE YUCATAN PENINSULA

R. A. EMERSON

FOREWORD

In January and February of 1935, Professor R. A. Emerson, of Cornell University, and Mr. J. H. Kempton, then of the U. S. Department of Agriculture, studied maize farming among the Maya Indians at the request of the Carnegie Institution. The following report, circulated in mimeographed form under Dr. Emerson's name, is one of the tangible results of this preliminary survey. Though it has been cited in at least two bibliographies its very existence has been unsuspected by many students of maize. We are indebted to Mrs. Ida K. Langman, of the Academy of Natural Sciences of Philadelphia, for supplying us with a copy, and to Dr. H. E. D. Pollock, of the Department of Archaeology of the Carnegie Institution, for granting permission to reprint the document.

Up until the time of his death Dr. Emerson was the heart and center of research in maize genetics. He was not only the outstanding authority; most of the other workers had either been trained under him or had been closely associated with the work of his laboratory. Mr. Kempton, on his part, has been identified with much of the research on maize which was carried on in the U. S. Department of Agriculture and had taken the lead in studying maize and its relatives in Latin America.

During the last decade, Mexico, in general, and Mexico's pattern of growing maize, in particular, have changed at an ever-accelerating rate. Dr. Emerson's report, though preliminary and informal, gives us an over-all picture of maize in an out-of-the-way part of Mexico fifteen years ago as seen through the eyes of the greatest maize scholar of his time.—EDGAR ANDERSON.

PURPOSE OF THE SURVEY

In the course of archeological studies of the ancient Maya civilization, conducted by the Carnegie Institution of Washington and other agencies, it has become important to estimate the density of population that could have been maintained by the agricultural system then in use. Is it possible that the Mayas of one or two thousand years ago could have used a more intensive type of agriculture than that employed by Mayas of the present day? Could the fact that large cities and their contributing territories were abandoned, some of them to be rehabilitated only after some hundreds of years, have been due even in part to the inadequacy of the agriculture of these regions? Could a possible decline in the productivity of the agricultural land have necessitated abandonment after a century or more? Was such postulated decline in soil fertility related casually to the system of agriculture in vogue?

It was not so much to find conclusive answers to such questions as these as it was to form an opinion of the possible value of a more thorough and sustained agronomic study as an aid in answering them that a preliminary survey of parts of the former Maya region was undertaken.

REGION COVERED BY THE SURVEY

The survey was conducted under the auspices of the Division of Historical Research of the Carnegie Institution of Washington and under the tutelage of Dr. S. G. Morley of the Chichen Itza project of that Institution. It was begun the latter part of January and continued to the end of February, 1935. The

personnel consisted of Mr. J. H. Kempton of the United States Department of Agriculture, and of the writer. Throughout the study they had the help of an interpreter and usually of a local milpero.

The study of milpas was begun at Piste in the central part of the state of Yucatan near Chichen Itza and about 120 kilometers from Merida. Trips between Merida and Chichen Itza by automobile and by train over different routes, a trip by train from Merida southeast to Peto about 150 kilometers, and another by train from Merida southwest to Campeche about 180 kilometers, afforded glimpses of the western half of the state of Yucatan and the northwestern part of the state of Campeche. From a number of places along these lines of railroad, milpas at distances ranging from a few up to 40 kilometers were visited by automobile, tram-car, mule cart, on horse-back, or afoot. Such points of departure were: Piste, Oxkutzkab, and Peto in the state of Yucatan, and Campeche in the state of Campeche.

TYPE OF COUNTRY VISITED

Topography.—The parts of Yucatan and of Campeche that were visited, as is said to be true of all of the northern part of the Yucatan peninsula, are a low, slightly undulating plain, broken in the southwestern part by ranges of low hills themselves only a few hundred feet above sea level. There is not even a suggestion of a river or brook in all that part of the peninsula visited.

Limestone rock.—The soil is underlaid throughout by a rather soft and porous limestone. Everywhere there appear outcrops of this rock. The sides and tops of small low knolls, often seen to be all rock, and the intervening areas, only a few meters less elevated than the knolls, exhibit many outcrops of rocks. In fact, it is never far from the surface to stratified rock. Although this soft limestone seems to harden on exposure after being taken from quarries, there are abundant evidences of its weathering to produce the usually scant soil. Everywhere exposed rocks are pitted with holes from the size of pin-heads to a meter across and half that deep. Both vertical and horizontal crevices of variable sizes are to be noted greater or less distances apart. Such crevices extend downward for considerable distances, perhaps even to the permanent water table which lies from a few to 50 or more meters below the surface, the distance apparently depending on the relative elevation of the surface. Numerous caves and even large caverns exist. Not infrequently these extend down to or considerably below the water table. When such caverns are open to the surface, they constitute the natural wells, *cenotes*, of the region, upon which the Mayas depend for their water supply.

Soils.—Evidences of the weathering of limestone rocks to produce soil are so universal that one is inclined to speculate on what would have been the nature of the land surface, had these rocks been exposed for ages to the alternate freezing and thawing in latitudes far to the north. Presumably the low plain would have been covered with some meters of fine loam instead of the scant soil covering now seen. And this might have resulted in a very different type of agriculture from that now prevailing.

On the numerous low knolls the soil is seldom more than a few centimeters deep and on many of them soil is seen only in pockets, or crevices in the rock. Crevices seem to be filled with surface soil and humus to considerable depths, as can be readily observed in recently worked stone quarries. Between the knolls the soil may be a half meter in depth, in some places more, and in many places much less than that. The only relatively deep soils observed are those bordering the ranges of low hills in the southwestern part of the area visited. At Oxkutzkab such border soils were said to be as much as five meters deep. The near absence of surface stone and the luxuriant growth and productivity of citrus trees in this region make such an estimate seem not unreasonable. Evidently the heaviest rains have carried down to the plain enough sediment to build up a relatively deep soil at the foot of the hills. Yet, there is little evidence of even temporary waterways on the hillsides and no evidence whatever of brooks paralleling the base of the hills or leading away from them. The water presumably spreads out in a thin sheet over the plain, depositing much of its sediment before disappearing into rock crevices. These bands of deeper soil at the base of the hills are of very minor importance for the region as a whole, for they are seldom as much as a kilometer wide and in many places are very narrow.

The surface soil, to a depth of a few centimeters on land on which the bush has been undisturbed for from ten to twenty years, is made up largely of decaying vegetable matter. During the dry winter season there is a sparse covering of dry leaves, nowhere the heavy covering seen in northern forests. Beneath this layer of leaves is a shallow layer of partly decayed vegetable matter and below that the red or brown loam. Evidently the relatively high temperature and considerable moisture of the region induce such rapid decay of the fallen leaves that no deep layer of decaying vegetable matter ever accumulates.

Climate.—The entire peninsula of Yucatan lies within the tropics, the northernmost part being somewhat below the 22nd parallel of latitude. The rainfall is light in the extreme northern and northwestern parts of the peninsula. Near Merida and along the gulf coast as far south as Campeche, the annual rainfall is said to be not over 18 to 20 inches. At Chichen Itza the annual precipitation approaches 50 inches. The year is divided into two seasons, a summer rainy season of about five months, usually from May to September inclusive but sometimes beginning nearly a month earlier or a month later, and a dry winter season of about seven months from October to April inclusive.

Some of the weather records kept at Chichen Itza for the past nine or ten years were examined. The total precipitation for 1933 was 50.1 inches and for 1934, 46.6 inches. During the five months, May to September, of 1933, 86 per cent of the year's rain fell; during the same months of 1934, only 73 per cent of the annual rainfall was recorded. Of the 730 days of the two-year period, rain fell on 275 days, 185 of them in the two five-month summer seasons. The maximum rainfall for one day, 4.75 inches, occurred in September, 1933. One-half inch or more of rain fell on 56 of the 275 rainy days, and 46 of the 56 were in the May–

September periods. During the two-year period there were 168 days on which .2 inches or less of rain fell, 102 of them having been in the five-month summer seasons.

The mean of the maximum daily temperatures for the years 1933 and 1934 at Chichen Itza was 91.6° F., and the mean of the daily minimum temperatures was 65.6° F. The highest temperatures occurred in March, April, and early May, maximum temperatures of 101°, 103° and 105° F. respectively having been recorded for these months in 1933. When the rainy season begins the maximum temperatures are not as high. Minimum temperatures are lowest during the period from late November to early March. During 1933 the lowest temperature recorded was 47° F., which occurred twice in December; in 1934, 44° was recorded twice in March, and 43° once in December. The lowest temperature on record was 40° F. on January 27, 1935.

Vegetation.—Except for land in crops, the whole of the northwestern part of the Yucatan peninsula is covered by "bush". This consists for the most part of trees and of vines which cling to the trees. In land not in crops for ten to twenty years, the dominant trees are 10 to 15 meters high and 10 to 20 centimeters in diameter. Under these are many smaller trees that have died or been suppressed by the shade of the larger trees. Relatively few annual weeds and almost no grasses are seen in any heavy bush. Both of these occur, however, along trails and in the more open places in the bush.

In bush of only a few years' growth, many annual weeds and small vines are to be seen. Among these are amaranths, numerous composites, and several kinds of bindweed. As the trees grow and shade the ground more and more, these weeds are less and less common. Even in very recently abandoned milpas little grass is seen except in the extreme northern and western parts of the area visited. Here the many large henequen haciendas, in which the bush has been kept cut for ten to fifteen years, apparently return to bush less rapidly when abandoned and more grass is seen.

The surface outcrop of rock does not seem to interfere much with tree growth. It is not uncommon to see large trees with roots exposed on the rock surface for several meters. Evidently the roots grow out in the thin cover of soil until a crevice is reached, then turn abruptly downward. In rock quarries roots 5 centimeters in diameter have been found 2–3 meters beneath the land surface.

THE MILPA SYSTEM OF AGRICULTURE

Location of milpas.—Difficulty was experienced in learning why a Maya Indian selects a particular site for his milpa. The Mexican Government, in some regions at least, has assigned areas of bush around the several villages for the use of the inhabitants of those villages. If a milpa is made beyond the designated area on Federal land, a tax is exacted by the Government. Milpas have been visited which were 8 to 12 kilometers from the village in which the milperos making them lived. The factors that seem to govern the selection of a site are: type of soil, ease of

cutting the bush, nearness to the village, the presence of water, etc. There are undoubtedly differences in bush soils, though it is not easy to see the difference between what the milpero calls good and poor soils. There appears to be a size range in bush trees on either side of which cutting the trees is more difficult. Trees of more than say 15 centimeters diameter are not easily cut with the small axes of milperos. Likewise, small trees sometimes bend under blows of the axe and must be cut with machetes. Moreover, and perhaps of more importance, in bush made up largely of small trees, there are many more trees per unit area.

When milpas are made near a village, the milperos return to the village after their day's work. When a milpa is more than an hour's walk away—5 or 6 kilometers—the milpero usually moves to his milpa during the periods when he must work more or less steadily. In such instances, nearness to water, a *cenote* or a well, is of prime importance. The necessity of building a fence around a milpa, if near a village, where cattle and horses have free range, may often be a factor influencing the selection of a site far enough away to obviate the necessity for this extra labor.

Making the Milpa.—A site having been selected, the milpero cuts the bush in the early part of the dry season, November to January, and allows the trees to lie as cut until they are dry enough to burn. The largest trees are usually left standing. Among these are the *ramon* tree, the leaves and small branches of which are much used as forage for domestic animals, and the *zapote,* from which the chicle is obtained. The few palm trees, the leaves of which furnish the thatch for Maya huts, are almost never cut. The trees are usually cut at about waist height. Where fences are necessary, many of the smaller trees near the periphery of the milpa are left to be cut as needed for construction of the brush fence. In some milpas, some of the smaller trees are cut at heights of 2 or more meters, the stumps later serving as supports for the bean vines grown with the maize.

In March or April, before the rainy season, the cut and then dry bush is burned. The milpero waits for a day of relatively strong wind and starts his fire on the windward side of the milpa. By this time many of the stumps left standing have sprouts a meter or more long. This new growth is killed by the fire, and if the bush were a heavy one, the stumps and the large uncut trees may be killed, but usually, though considerably burned, many of them are left alive. Lundell, in his "Preliminary sketch of the phytogeography of the Yucatan peninsula," refers repeatedly to devastating fires which not only burn the felled bush but also sweep through the whole countryside. In this visit to northwestern Yucatan, absolutely no evidence of such forest fires was seen. Particular attention was given to this possibility throughout the trip; and in no instance was evidence found of milpa fires having burned for more than a few meters into the surrounding green bush. This study was made before the season of milpa burning, but one large milpa fire near Chichen Itza was watched. Even with a strong wind, the fire burned only the dry leaves and small dead trees for only a few meters beyond the felled bush; and the fire had ceased to burn in the uncut bush while it was still burning hotly

in the trunks of the larger felled trees. Sometimes a milpero takes the precaution of removing the cut bush around the edges of his milpa for a few meters before setting the fire, but most often this precaution is to protect from fire his newly erected brush fence. And perhaps this measure is only apparently one of precaution; the fence is most easily built with the cut bush that is nearest it.

When the rainy season begins, which may be in April or as late as the end of May, the maize is planted. A sharpened stick, usually with a metal point, is used to make a hole in the ground. In this are dropped four or five kernels of maize. Seeds of a native squash and of the common bean (always a black-seeded one) or of a lima bean are mixed with the maize and all are planted together at random. No attempt is made to arrange the hills in rows, and they are spaced irregularly averaging probably a little less than a meter and a half apart. Not infrequently hills are planted in narrow rock crevices or in the deeper pockets in the surface limestone. If this were not done, considerable areas on the low knolls could not be planted at all. Maize seems to grow in rock crevices as well as trees do. In the deeper soils at the base of the range of hills in the western part of the area visited, maize is planted in rows about one and a half meters apart with hills not over half a meter apart in the rows.

Sprouts of tree stumps and weeds that appear in a first-year milpa are cut with a *machete* from once to three times during the growing season of the maize. Very rarely is this done three times and probably more often once than twice. By harvest time the weeds and sprouts have grown to a length of from 1 to 3 meters. When the maize ears begin to mature, the stalks are bent over below the ears, so that the upper part of the stalks, including the ears, hangs down; this is done, it is said, to protect the ears from rain and from birds.

The maize harvest extends over a considerable period of time. It is not uncommon for a milpero to harvest a basket of ears whenever the previously harvested basketful has been used up. By the early part of February, however, most of the maize has been harvested and stored. The ears are gathered into palm-leaf baskets, with the husks on, and piled near a thatched hut in the milpa. The part of the crop that is to be used or sold at once is husked and shelled. Ears that are stored for any considerable period are left in the husks. A crib of stocks is built a little above the dirt floor of the storage hut, and the ears are packed in it tightly in a vertical position with the tips downward. This method of storage is said to lessen injury from rodents and insects.

In preparing a milpa for a second crop of maize, the weeds, stump sprouts, and maize stalks are not cut early in the dry season as was the bush the year before. The cutting is delayed until toward the end of the dry season, it was said because: (1) The small cut stems dry out quickly and therefore need no long drying period; (2) if cut early, more weeds and stump sprouts would grow before burning; and (3) the relatively small amount of trash does not produce a sufficiently hot fire to kill late-grown weeds and sprouts. As a matter of fact, this trash has to be piled as cut in order to insure its burning at all. A serious difficulty arising from this

delayed cutting, seemingly overlooked by the Maya milpero, is that it affords time for the ripening and dispersal of an abundant crop of weed seeds which are not destroyed in any large measure by the fires which burn the piled trash.

The first-year milpa, having been cleared and burned, a second maize crop is planted and tended just as the first one was. For the reason noted above, the weeds on a second-year milpa are much more abundant than on a first-year one. On visiting a milpa it was rarely difficult to decide at once whether it was a first- or a second-year one, using relative abundance of weeds as the sole criterion.

Occasionally, maize is grown on the same milpa for three consecutive years. On the narrow belts of deeper soil at the base of ranges of hills, maize is sometimes grown on the same milpa for four years. But, in an overwhelming percentage of cases, two years is the limit. The milpa is then abandoned to return to bush and a new one prepared by cutting and burning another area of bush. The length of time that a piece of land is left in bush before being cut again for a milpa varies greatly. Rarely, this period is as short as four or five years, and in some instances it is as long as fifteen or twenty years. There is insufficient evidence upon which to base a positive statement of the average length of this bush period, but it is probably not far from ten years. It would seem that the essential factor is a length of time sufficient for the dominant trees to reach a size satisfactory for cutting, and to choke out the smaller bush, and incidentally the annual weeds also.

YIELDS OF MAIZE GROWN BY THE MILPA SYSTEM

As in other places, maize yields in Yucatan vary from season to season. Throughout much of the area visited 1–1½ *cargas* per *mecate* is a good yield for a first-year milpa, and one or a little less than one for a second-year milpa. It should be explained that a *carga* is 42 kilos, or about 93 pounds, approximately 1⅔ bushels, and that a *mecate* is a plot of land 20 × 20 meters, or 400 sq. meters, almost one-tenth of an acre. While yields of 15 to 20 bushels per acre might well be regarded as unsatisfactory to a farmer in the corn belt of the United States, the surprising thing is that so good yields are obtained under the conditions prevailing in Yucatan.

DECLINE IN MAIZE YIELDS

That in general the yield of maize is somewhat less in a second-year than in a first-year milpa is everywhere evident. The bearing of this fact on the customary abandonment of a milpa after the second crop and its possible bearing on the withdrawal from a whole region by the ancient Mayas makes its cause or causes worth more than passing notice.

Soil depletion.—An opinion, apparently somewhat generally held, is that the system of agriculture now practiced by the Mayas results in rapid depletion of soil fertility. Lundell, in his "Phytogeography of Yucatan," says:

> The ashes are the only fertilizer the soil receives, so it is quickly exhausted. Little humus remains after fires have swept the land. The crop is best the first year; the second year it falls off, and in either the third or fourth year the clearing is abandoned and another site is chosen. The abandoned milpas are again placed in cultivation after a lapse of several years, during which interval the fertility of the soil is partly restored by the rank vegetation. Apparently continued rotation leads to complete soil exhaustion . . . .

Since the trees of northern and western Yucatan are hardwoods, and ashes from their burning undoubtedly provide readily available mineral nutrients for the first crop of maize, it seems unlikely that there can be much leaching of these nutrients, for, even after the maize is ripe, the weeds and stump sprouts continue to grow and are not cut until late in spring. It is true also that the fire which burns the dried bush in preparation for the first-year crop burns the few leaves then on the ground and destroys some of the scant layer of humus. Rarely, however, does this destruction of humus extend for more than a couple of centimeters below the soil surface, and that far only where relatively large tree trunks have burned. The burning of stalks, weeds, and stump sprouts preparatory to the second crop has little effect on the remaining humus. This vegetation is so scanty that it has to be piled to insure its burning at all.

One with an agronomic background finds it difficult to believe that milpas, after two crops of maize, have been abandoned because of soil depletion, and equally difficult to conceive of soil fertility, once depleted, being restored by a few years of tree growth. Even without an agricultural background, one might reasonably question how such weeds as amaranths in a second-year milpa could grow to a height of 2–3 meters with a spread of branches nearly equal to their height if the soil were nearing exhaustion.

Weed competition.—In bush of several years standing, such as is felled for a first-year milpa, there are relatively few annual weeds, and these are found mainly along the narrow trails and in the more open parts of the bush. Many of the seeds of these annuals are undoubtedly killed by the intense heat of the burning slash. But some certainly escape, for there is always a considerable number of weeds in a first-year milpa. Since the earlier appearing weeds are cut usually only once, and that during the maize-growing season, weeds continue to grow long after the crop is ripe and are still flowering and only beginning to ripen seed in February; and since these late-growing weeds, along with the maize stalks and stump sprouts, are not cut until near the end of the dry season, there is opportunity for the ripening and dispersal of an abundant crop of seeds. Only a few large weeds may produce enough seed to stock the whole milpa. The burning of scattered piles of trash late in spring can have little destructive effect on the weed seeds which by that time are widely spread over the soil. The system is an ideal one for stocking the second-year milpa with noxious weeds. It seems almost too

obvious to require statement that weed competition rather than soil depletion is the factor primarily responsible for the lessened yield of the second-year milpa. It seems equally clear that tree growth after abandonment of a milpa functions primarily in choking annual weeds rather than in restoring depleted soil fertility.

The labor differential between first-year and second-year milpas.—Statements of milperos agree that more time is required to cut the weeds during summer in a second-year than in a first-year milpa. Moreover, it takes materially more labor to cut, pile, and burn the maize stalks, weeds, and stump sprouts in preparation for a second-year milpa than to cut and burn the bush for a first year milpa. Only from careful records of labor requirements can this differential be accurately determined, but it would not be surprising to find that the preparation and care of a second-year milpa necessitate from one and a half to two times the amount of labor that a first-year milpa requires.

THE MILPA SYSTEM OF AGRICULTURE IN RELATION TO DENSITY OF POPULATION

Dr. Steggerda's study of the dietary of the Maya Indians of the village of Piste indicates that maize furnishes about 85 per cent of the Maya's diet. The problem of food supply adequate for a given population is, therefore, largely one of how much maize can be grown in the region. Dr. Steggerda's records indicate that an average Maya family of five requires annually about 30 cargas of maize. In so far as can be determined from a hurried survey such as this, the usual yield of maize is 1 to somewhat more than 1 carga per mecate, and an average size of milpa for one family is probably not far from 40 mecates. It would seem, therefore, that the Maya now grows enough maize for his family plus what the chickens, dogs, and other animals eat, with some to sell to provide the family with the cheap cotton clothes they wear and the few other purchased articles they require.

Since a milpa is used ordinarily for only two years and then abandoned, and if about a ten-year interval in bush is necessary before the land is again used for maize, a crop can be produced on the average about one year in six. In other words, about 17 per cent of the entire area might be in maize each year. This statement is based on the assumption that none of the land is unsuited to maize production—an assumption that is almost literally true for the parts of the Yucatan peninsula covered in this survey. The water problem could be solved by artificial wells, such as are now in use. What percentage of this area is now in milpas in any one year is not known. But going over the country by rail, automobile, mule cart, and on horse-back, one is impressed by the very small fraction of the country in milpas. This impression was strengthened by observations made in going by air over the entire northern part of Yucatan from Merida to the east coast of the peninsula. While only by accurate records of sample areas can one obtain the necessary information, it would surprise the writer if such records, when obtained, show so much as 1 per cent of the land in milpa at a given time.

If this guess is not too wild to be credited, 15 to 20 times as much maize might be produced each year as is now grown, thus supporting that many times as large a population as is now found in the Yucatan peninsula, and this without changing the present system of milpa agriculture. No evidence was found in this short-time survey to indicate that the present system of milpa agriculture could not be maintained indefinitely. It would seem, therefore, that 15 to 20 times as great a population as the rather sparse one now in existence could find an adequate food supply. Even this figure would probably fall far short of the tremendous density of ancient population postulated by some archeologists in moments of ultra enthusiasm. The factual bases for such estimates are unknown to the writer and are perhaps beyond the powers of comprehension of a mere maize specialist. They do, however, call for a consideration of the possibilities that, in ancient times, a more intensive type of agriculture may have been practiced.

In the territory covered by this survey, there is no evidence of the type of intensive agriculture inferred from mountain-side terraces such as those seen by the writer some years ago near Inca remains in Peru. Of course, no such things are to be expected in a low and flat country such as northern and western Yucatan.

Whether the ancient Mayas employed fertilizers other than the ashes from burned trees or used partly rotted vegetable matter as a manure—as the present-day Maya Indians certainly do not—it is idle to guess.

The advanced civilization of the ancient Mayas would certainly have been capable of inventing tillage implements. They had no beasts of burden, but the postulated population should have furnished man power enough to obviate the need of horses or oxen. Even though the ancient Mayas had no metal tools, they could have made plows and cultivators, as they did axes and knives, from stone and hard wood. But why waste time on such details? Even our modern steel implements of tillage could not possibly be used anywhere in Yucatan except in the deeper soils at the base of the ranges of hills. Even if the outcropping rock did not incapacitate such implements in the first half hour of use, the rocks would keep them from reaching the intervening soil pockets. The main basis for the opinion that ancient Maya agriculture was much like present-day milpa agriculture is the fact that no other type can be regarded as having a chance of successful use. The Mayas of today use the only method available; and the ancient Mayas presumably used the same system for the same reason.

There remains one possibility not yet discussed. Could the ancient Mayas have kept the land in maize more than two years at a time, perhaps many more than two? Or, could they have shortened the interval during which the land was abandoned to go back to bush? By either of these ways the percentage of the whole area in maize at any one time could have been correspondingly increased. The agronomic problem involved in such longer or more frequent use of the land for maize is largely one of greater weed competition resulting in lessened yields or of more labor per unit area to hold the weeds in check.

Information obtained from Maya milperos indicates that it requires from one and one-half to two times as much labor to care for a second-year as for a first-year milpa. Cutting the weeds, stalks, and sprouts in a milpa as soon as the maize is mature enough to harvest, and thus before the weed seeds have ripened and been scattered, instead of waiting as at present until near the end of the dry season, should materially lessen the weeds to be fought the next season. But there is no way of knowing whether the ancient Maya's routine differed from that in vogue at present.

How much time does a Maya spend in caring for a milpa large enough to supply his dependents with maize for the year? If the ancient Mayas used materially more than one-sixth of the land for maize each year, could the milperos have devoted enough time to their milpas to meet the weed problem involved? A milpero cuts about two mecates of high bush a day. In cutting the trash in preparation for a second-year milpa, he covers about the same amount of land, but this takes the greater part of a day, while cutting two mecates of bush for a first-year milpa seldom requires all day. Two mecates seem to be the day's stint, irrespective of how many hours of work are required. Rarely is more than one mecate cleaned of weeds in one day's work during the growing season of maize in a second-year milpa. Under the present system, therefore, to prepare land enough for the maize needed by one family—say 40 mecates, or about 4 acres—and to weed it once in summer requires about sixty days of labor for one man. Burning the felled trees or the weeds and stalks, planting, and harvesting could hardly require more than twenty days. It follows that the present-day Maya milpero has about three-fourths of his time free from the labor necessarily connected with his milpa. The ancient Maya milpera grew cotton as well as maize, but the Maya of today grows enough more corn so that he can sell some in order to buy cotton cloth. Moreover, the ancient milperos must have grown enough maize for their priests and rulers in addition to the requirements of their own families. But even so, the ancients could have spent more time on their milpas than do their descendants of the present time, and still have had much time in which to build pyramids, temples, and the like. All this, if true, suggests that the present milpa system of agriculture, with only minor modifications, could have supported a very much greater population than is found today in the Yucatan peninsula—how much greater only careful long continued studies can determine.

What effects longer and more frequent use of the land for maize growing would have on soil fertility is beyond the writer's ability at guessing. Certainly soil erosion could have played no part in bringing about the abandonment of a low, flat region like that around Chichen Itza. There is no evidence whatever, so far as one who is not a geologist can determine, to indicate the presence of such "washes" as one sees commonly in the much drier regions, deserts, of California. But these regions are bordered by real mountains, not merely the low hills of Yucatan; and the steepness of their slopes is a surprise to any automobile driver who is likely to have his engine stall on what seems almost level ground.

The absence of erosion in northern and western Yucatan is no argument against the possibility that erosion was an important factor in causing the abandonment of the higher and more broken regions farther south where the old-empire Mayas flourished for a time only to abandon the area later and migrate to the low lands of Yucatan. Whether or not the erosion theory is the correct answer to the abandonment of the territory of the old-empire Mayas, it is now serving a useful purpose as the goblin of the present erosion campaign in the United States.

RECOMMENDATIONS

The survey here reported was only a preliminary study. Although statements of milperos are perhaps correct, many of the figures given here are at best only estimates and some of them are guesses, perhaps very poor guesses. At best a hurried survey could not be expected to do more than to indicate what the elements of the problem are and to suggest the kinds of accurate information needed.

The writer is convinced that weed competition and the labor involved in weed control is a more important factor than soil exhaustion, and yet, the latter might enter to a greater or less degree, particularly if the land were used for maize culture for relatively long periods and at relatively frequent intervals. The only way to get reliable information concerning the possible depletion of soil fertility by maize culture is to conduct, for several years, a carefully planned and carefully executed field-plot experiment. But this would require the services of a man trained in modern agronomic technique for at least part of each year, and of a trustworthy helper to keep detailed records during the growing season.

But there are problems of perhaps more immediate importance which should be undertaken at once, if their solution is of enough importance archeologically to warrant the expense involved. And, for the solution of these problems also, it is of prime importance to have a well-trained man with a well-founded agronomic background. Such a study should provide accurate information to take the place of the hear-say evidence, the estimates, and the guesses presented in this report.

It would seem sufficient to select six or eight sample areas, such as the territory contributory to Piste already studied in part by Dr. Steggerda. It is important to know the number of people gaining their support in a given area, the amount of maize produced and used for food by them and their domestic animals, or sold in order that other necessities may be purchased, the number of mecates cultivated in order to provide this maize, and the relation that the area of all the milpas bears to the entire area. Accurate information should be obtained also respecting the hours of labor per unit area devoted to each separate operation involved and in the preparation and care of milpas.

If a field-plot experiment is undertaken, one series of plots should be kept free from weeds at whatever cost, while another series is cared for as the Mayas now tend their milpas. Such an experiment should afford information not only in respect to possible soil depletion, as measured by maize yields, but the labor records should be of value in appraising the possibility that the ancient Mayas may have kept the land in milpas a greater percentage of the time than is now done.

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MAY, 1953

A Contribution to the Lichen Flora of Arizona and New Mexico . . . . . Emanuel D. Rudolph 63–72
The Analysis of Suspected Hybrids, as Illustrated by *Berberis* × *gladwynensis* . . . . . Edgar Anderson 73–78
Variation in Cob Morphology among Certain Archaeological and Ethnological Races of Maize . . . . . Norton H. Nickerson 79–111
The Cytology, Morphology, and Systematic Relationships of *Delphinium* × *Belladonna* Hort. ex Bergm. . . . . Marilyn Amy Gage 113–186

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A CONTRIBUTION TO THE LICHEN FLORA OF ARIZONA AND NEW MEXICO

EMANUEL D. RUDOLPH*

The lichen flora of the states of Arizona and New Mexico is much less known than that of many other sections of the United States. In addition to the references on distribution given in the standard works of Tuckerman (1882, 1888) and Fink (1935), there are only scattered papers in the literature which are concerned with the lichens of these states. Tuckerman, in 1860 and 1862, reported on the collections made by Fendler near Santa Fe. When these records were brought together in 1866, several collections made by Wright in New Mexico were added. Tuckerman (1878) also wrote up some Arizona collections made by the U. S. Geological Survey of the 100th Meridian. It was not until some time later that Fink (1909, 1909a) studied the lichens of the vicinity of Tucson, Arizona, from where some new species were described by Zahlbruckner (1908, '09). In 1932 Bouly de Lesdain published an account of lichen collections from the vicinity of Las Vegas, New Mexico, made by Brother Arsène Brouard, and, in 1942, on further collections from the vicinity of Santa Fe. Magnusson (1929, 1937) treated the *Acarospora* of Brother Arsène Brouard. Herre (1944, 1950) has provided additional information on the lichen flora of New Mexico from San Miguel and Sierra counties. Finally, Darrow (1950) has reported on the arboreal lichen flora of southeastern Arizona. The present paper includes forms from some new localities in Arizona and New Mexico of which three are new species and a number are additions to the flora.

This compilation is the result of a study of two collections: (1) that of Dr. Robert A. Darrow made in various localities in southeastern Arizona in 1933 and 1934, and in the 1940's which includes only saxicolous and terricolous forms; (2) that made by Mr. and Mrs. Francis Elmore at Chaco Canyon National Monument in northwestern New Mexico in 1952. The latter is for the most part saxicolous, but a few corticolous forms are included. Thus most of these lichens are crustaceous rock-inhabiting ones which form a conspicuous element in the vegetation of these arid mountainous regions.

* Missouri Botanical Garden.

The arrangement and nomenclature, wherever possible, follows that of Fink (1935). The treatment of *Acarospora* is in accord with that of Magnusson (1929a). A complete set of specimens is on deposit in the herbarium of the Missouri Botanical Garden.

I should like to thank Dr. Carroll W. Dodge for his valuable guidance and assistance throughout this study.

LIST OF SPECIES

VERRUCARIA FUSCELLA (Turn.) Ach.—ARIZONA: Tucson, on caliche, 2500 ft., Dec. 4, 1933, *Darrow 572;* Tucson Mts., on volcanic rock, 3000 ft., March 11, 1934, *Darrow 746.* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16 & 20, Feb. 28, 1952, *Elmore.*

STAUROTHELE UMBRINA (Ach.) Tuck.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *Elmore.*

DERMATOCARPON POLYPHYLLUM (Wulf.) Dalla Torre & Sarnth.—ARIZONA: Pima Co., Rincon Mts., on shale, 4500 ft., March 4, 1934, *Darrow 697.*

DERMATOCARPON RUPICOLA Zahlbr.—ARIZONA: Tucson Mts., on andesite, 3500 ft., March 15, 1934, *Darrow 690.*

ENDOCARPON PUSILLUM Hedw.—ARIZONA: Tucson Mts., on caliche, 3000 ft., March 11, 1934, *Darrow 745.*

ARTHOPYRENIA HALODYTES (Nyl.) Arn.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

PYRENULA NITIDA (Weig.) Ach.—NEW MEXICO: Chaco Canyon, on greasewood *(Sarcobatus vermiculatus* (Hook.) Torr.*)*, 6200 ft., Jan. 20, 1952, *Elmore.*

URCEOLARIA SCRUPOSA (Schreb.) Ach. var. BRYOPHILA (Ehrh.) Ach.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on *Cladonia* primary thalli, Dec. 24, 1933, *Darrow 537.*

LEPTOGIUM APALACHENSE Nyl.—ARIZONA: Pima Co., Rincon Mts., on shale, 4500 ft., March 4, 1934, *Darrow 698.*

LEPTOGIUM BURGESSII (L.) Mont.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on soil, Dec. 24, 1933, *Darrow 533.*

PLACYNTHIUM MICROPHYLLIZUM (Nyl.) Hasse—ARIZONA: Tucson, on soil, 2500 ft., Nov. 26, 1933, Apr. 5, 1934, *Darrow 527, 691;* Pima Co., Cortaro, on soil, 3000 ft., Nov. 26, 1933, *Darrow 528;* Pima Co., Rincon Mts., on soil, 3500 ft., March 4, 1934, *Darrow 740, 741.*

LECIDEA BRANDEGEI Tuck.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

LECIDEA PARASEMA Ach.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

LECIDEA PLANA (Lahm) Nyl.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

LECIDEA VORTICOSA (Floerke) Koerb.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

RHIZOCARPON DISPORUM (Naeg.) Müll. Arg.—ARIZONA: Mt. Lemmon, Santa Catalina Mts., on marble, 8500 ft., April 1, 1934, *Darrow 721.*

ACAROSPORA AMERICANA H. Magn.—ARIZONA: Tucson Mts., on volcanic rock, March 11, 1934, *Darrow 747;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

ACAROSPORA COLORADINA H. Magn.—ARIZONA: Tucson Mts., on volcanic rock, 3000 ft., March 11, 1934, *Darrow 746.*

ACAROSPORA OXYTONA (Ach.) Mass.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *Elmore.*

ACAROSPORA PELTASTICA Zahlbr.—ARIZONA: Tucson Mts., on volcanic rock, 3000 ft., March 11, 1934, *Darrow 736;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *Elmore.*

ACAROSPORA STRIGATA (Nyl.) Jatta—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16 & 20, 1952, *Elmore.*

ACAROSPORA TENEBRICA H. Magn.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

ACAROSPORA WASHINGTONENSIS H. Magn.—ARIZONA: Pima Co., Rincon Mts., on schist, 4500 ft., March 4, 1934, *Darrow 788.*

PERTUSARIA FLAVICUNDA Tuck.—ARIZONA: Santa Rita Mts., on igneous rock, 7200 ft., Aug. 14, 1934, *Darrow 820.*

LECANORA ATRA (Huds.) Ach.—ARIZONA: Patagonia Mts., on granite, 5500 ft., Oct. 6, 1946, *Darrow 4252.*

LECANORA CENISIA Ach.—ARIZONA: Santa Rita Mts., on igneous rock, 7000 ft., July 16, 1934, *Darrow 796.*

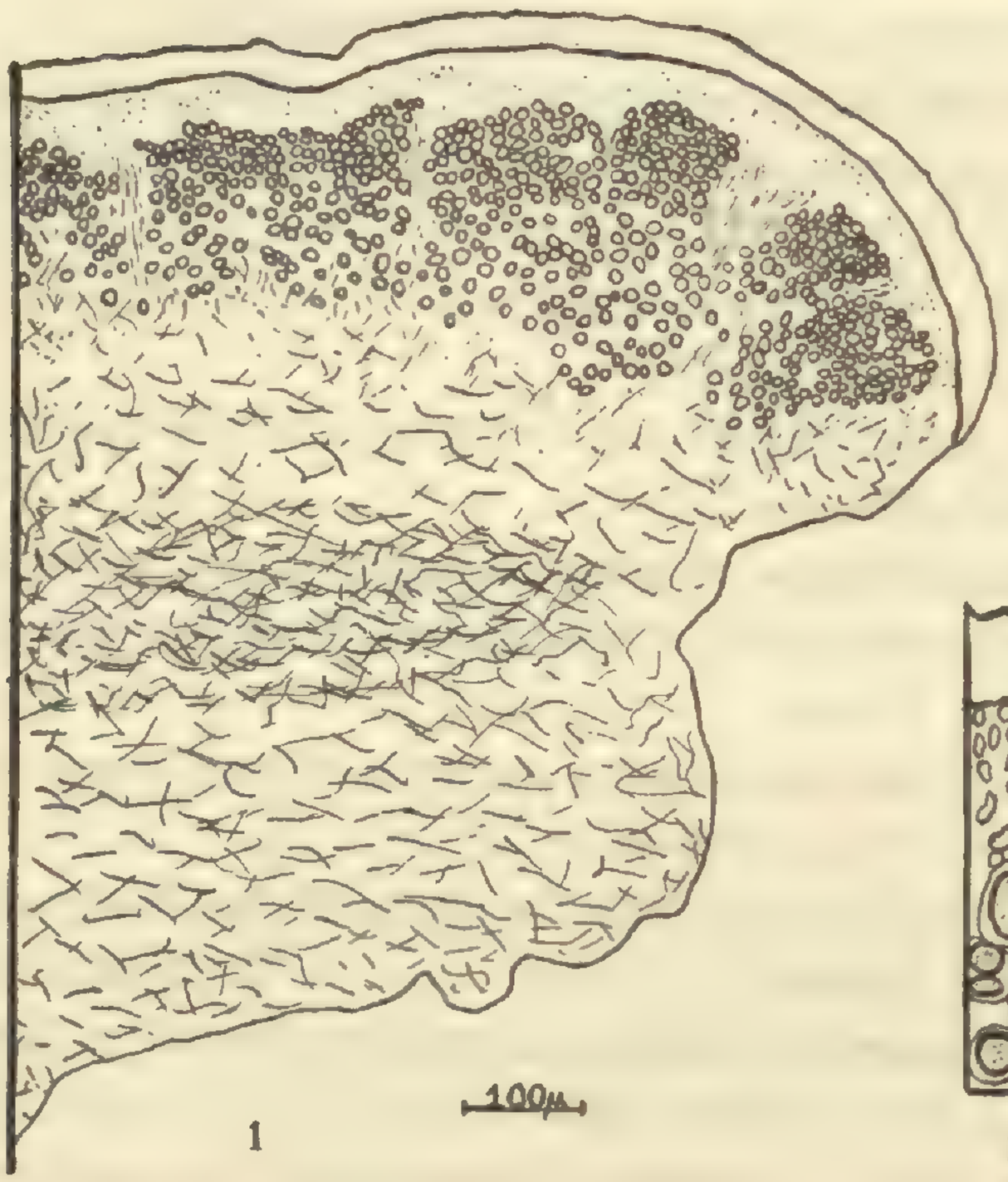
LECANORA CONTORTA (Hoffm.) Stiz.—ARIZONA: Mt. Lemmon, Santa Catalina Mts., on quartz, 8500 ft., April 1, 1934, *Darrow 724.*

LECANORA DIFFRACTA Ach.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on granite, 6500 ft., Dec. 24, 1933, *Darrow 470.*

LECANORA (ASPICILIA) **elmorei** E. Rud., var. nov.—TYPE: NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *T. & F. Elmore.*

Thallus determinatus, laevigatus, obscure olivaceus, areolatus, areolis crassis convexisque, 1–2 mm. diametro; cortex 31–41 μ crassitudine, K—, fastigiatus, dimidia parte corticis crassitudine strato gelifacto tectus, hyphis circa 3 μ diametro; algae ad *Trebouxiam* pertinentes, cellulis ad 38 μ diametro, in strato non continuo, 100–170 μ crassitudine sub cortice; medulla hyphis laxe contextis circa 4 μ diametro. Apothecia in areolis crassioribus immersa, unum vel plura in quavis areola, amphithecio prominente, persistente, crasso, thallo concolore, disco concavo obscure olivaceo-alutaceo pulverulento; hypothecium indistinctum sed densum; thecium 150–171 μ altitudine; paraphyses simplices, septatae, circa 2 μ diametro, apicibus clavatis; asci 71.5–100.0 $\times$ 14.3–15.7 μ, clavati, apicibus incrassatis; sporae uniseriate, 3–4-nae, sphaericae, 17.4–24.4 μ diametro, granulosae, episporis tenuibus.

Thallus determinate, smooth, deep olive, closely areolate, the areolae thick and convex, 1–2 mm. in diameter; cortex fastigiate, 31–41 μ thick, covered by a



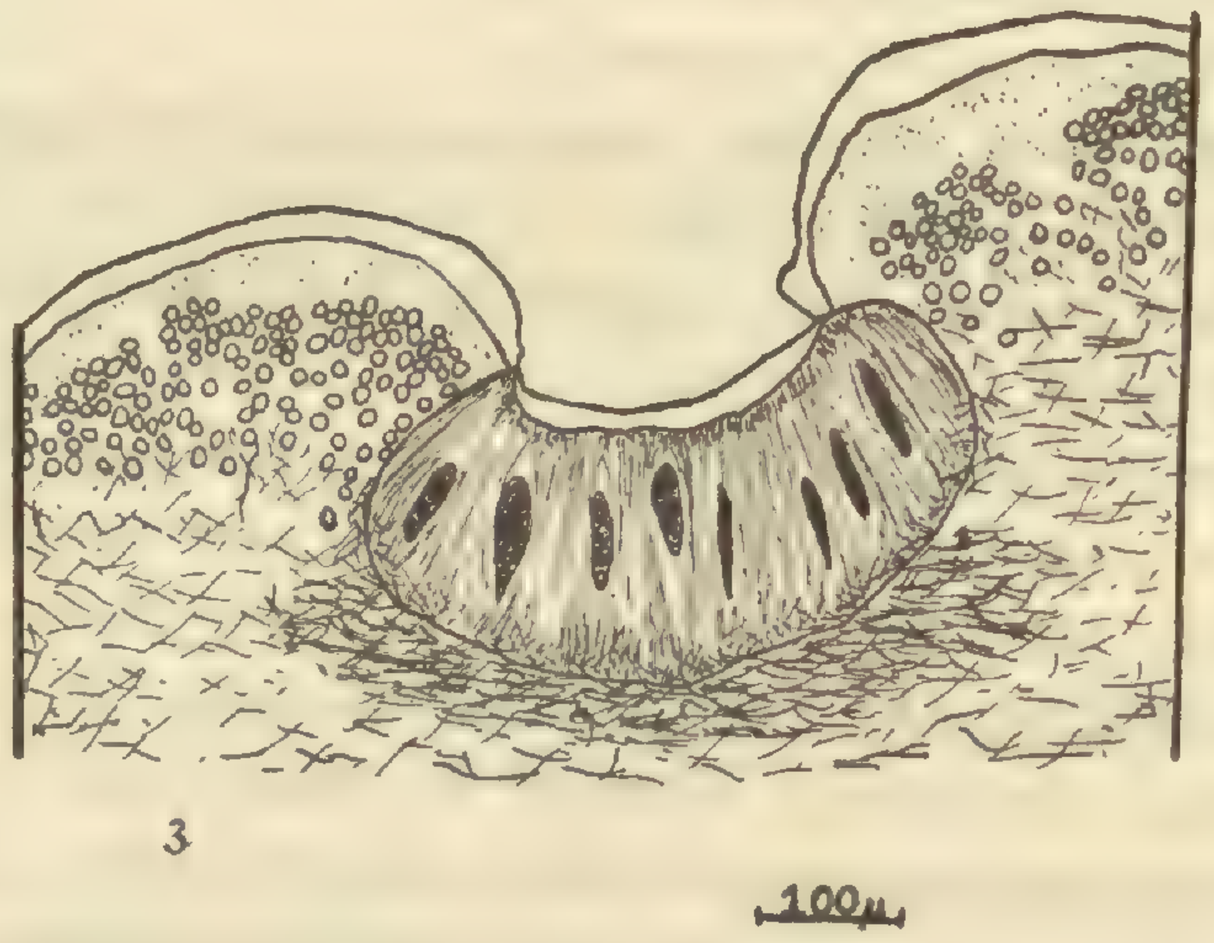


Fig. 1. *Lecanora elmorei* E. Rud.

1. Section of thallus.
2. Enlarged section showing cortex.
3. Section of an apothecium.
4. Ascus with associated paraphyses.

gelatinous layer about half the thickness of the cortex, KOH—, the hyphae approximately 3 μ thick; algae *Trebouxia*, forming a layer 100–170 μ thick below the cortex, broken into vertically rectangular patches separated by fungous hyphae, the cells globular to slightly angular, 10–38 μ in diameter; medulla of loosely woven hyphae about 4 μ in diameter. Apothecia sunken, the margin formed of the remaining part of the aerolae, one to several per areolae, the disc very concave, dark olive-buff, appearing powdery; margin persistent, raised and thick, thalline, colored like the thallus; epithecium of gelatinous tips of paraphyses; hypothecium indistinct, slightly denser than the underlying tissues; thecium 150–171 μ thick, the paraphyses simple, filiform, septate, about 2 μ thick, the tips swollen. Asci clavate, 71.5–100.0 $\times$ 14.3–15.7 μ wide, hyaline tips present in many; spores uniseriate, 3–4 per ascus, globose, 17.4–24.4 μ in diameter, mostly coarsely granular, the epispores thin.

This new species is easily distinguished by its 3–4 globose spores per ascus and by having *Trebouxia* as its alga. The globose-spored species *Lecanora praecrenata* Nyl., with its diffuse, whitish, indeterminate thallus and sessile brown apothecia, contrasts easily with the thick, closely areolate, deep-olive thallus and sunken apothecia of the present species.

LECANORA EPULOTICA (Ach.) Leighton—ARIZONA: Santa Rita Mts., on igneous rock, 6500 ft., July 1, 1934, *Darrow 814.*

LECANORA FRUSTULOSA (Dicks.) Ach.—ARIZONA: Carr Canyon, Huachuca Mts., on marble, 5600 ft., June 12, 1945, *Darrow 4236.*

LECANORA MELAENA (Hedlung) Fink—ARIZONA: Tucson Mts., on calcareous rock, March 25, 1934, *Darrow 682.*

LECANORA PARISENSIS Nyl.—NEW MEXICO: Chaco Canyon, on greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), 6200 ft., Feb. 28, 1952, *Elmore.*

LECANORA POLYTROPA (Ehrh.) Rabh.—ARIZONA: Santa Rita Mts., Pima Co., on igneous rock, 4500 ft., Aug. 14, 1934, *Darrow 819.*

LECANORA THAMNOPLACA Tuck.—ARIZONA: Santa Rita Mts., on igneous rock, 7000 ft., Aug. 14, 1934, *Darrow 822;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

PARMELIA NOVO-MEXICANA Gyeln.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

CALOPLACA **arizonica** E. Rud. sp. nov.—TYPE: ARIZONA: Cortaro, on rhyolite, 3000 ft., Nov. 26, 1933, *R. A. Darrow 521.*

Thallus areolatus, fuscus; areolae 0.5–1.0 mm., dispersae; cortex circa 18 μ, fastigiatus, strato gelifacto tectus, K obscure purpurascens; algae protococcoideae ad 10 μ diametro, cellulis sphaericis vel subangulosis, in strato 90–130 μ crassitudine sub cortice; medulla hyphis laxe intertextis crystallis saxi impleta. Apothecia 0.2–0.6 mm. diametro, orbiculata, disco ferrigineo-aurantiaco, amphithecio distincto, persistente, tenui, thallo concolore; epithecium crystallis brunneo-luteis inspersum; hypothecium hyalinum, centro circa 70 μ altitudine; thecium 63–87 μ altitudine; paraphyses filiformes, 1.7 μ diametro, simplices, septatae; asci 24–42 $\times$ 7–11 μ,

Fig. 2. *Caloplaca arizonica* E. Rud.

1. Section of thallus.
2. Enlarged section showing cortex.
3. Section of an apothecium.
4. Ascus with associated paraphyses.
5. Ascospores.

clavati; sporae 8-nae, 8.7–12.2 × 3.5–5.2 μ, polari-biloculares, isthmo circa 3 μ longitudine, uni- vel biseriales.

Thallus indeterminate, aerolate, fuscous, the areolae 0.5–1.0 mm., often quite far apart; cortex about 18 μ thick, with a gelatinous covering, fastigiate, KOH dark purple; algae protococcoid, forming a layer 90–130 μ thick below the cortex, the cells round to angular, 5–10 μ in diameter; medulla of loosely woven hyphae about 3 μ thick, containing numerous small rock crystals. Apothecia circular, 0.2–0.6 mm., disc brownish-orange, the margin persistent, thin, of the same color as the thallus; algae in the margin and in a layer below the hypothecium; epithecium incrusted with brownish-yellow crystals, about 13 μ thick; hypothecium hyaline, about 70 μ thick at center; thecium 63–87 μ high; paraphyses filiform, septate, about 1.7 μ thick, unbranched. Asci clavate, 24–42 × 7–11 μ; spores 8, uni- or biseriate, polar-bilocular, 8.7–12.2 × 3.5–5.2 μ, the isthmus about 3 μ long.

This species somewhat resembles *Caloplaca cinnabarina* (Ach.) Zahlbr., but can be distinguished by its relatively fewer and more dispersed apothecia, darker thallus, and narrower spores.

CALOPLACA CERINA (Ehrh.) T. Fries—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

CALOPLACA CINNABARINA (Ach.) Zahlbr.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on granite, 6500 ft., Dec. 24, 1933, *Darrow 471.*

CALOPLACA ELEGANS (Link) T. Fries—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16 & 20, Feb. 28, 1952, *Elmore.*

CALOPLACA FESTIVA (Ach.) Zwackh.—ARIZONA: Miller Canyon, Huachuca Mts., on igneous rock, 6300 ft., June 14, 1945, *Darrow 4243.*

CALOPLACA FULGENS (Swartz) Koerb.—ARIZONA: Nogales, on calcareous rock, 4000 ft., Oct. 6, 1946, *Darrow 4261;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

CALOPLACA LOBULATA (Floerke) Hellb.—ARIZONA: Pima Co., Rincon Mts., on granite, 4000 ft., March 4, 1934, *Darrow 785.*

CALOPLACA MODESTA (Zahlbr.) Fink—ARIZONA: Tucson Mts., on calcareous rock, 3000 ft., March 19, 1934, *Darrow 730;* Pima Co., Coyote Mts., on granite, 3200 ft., Feb. 16, 1945, *Darrow 4266.*

TELOSCHISTES PARIETINUS (L.) Norm.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

BUELLIA BLUMERI Zahlbr.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on igneous rock, 6500 ft., Dec. 24, 1933, *Darrow 477.*

BUELLIA RETROVERTENS Tuck.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on granite, 6500 ft., Dec. 24, 1933, *Darrow 489;* Tucson Mts., on volcanic rock, 3000 ft., March 19, 1934, *Darrow 736;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

RINODINA **darrovii** E. Rud. sp. nov.—TYPE: ARIZONA: Santa Catalina Mts., on ground and moss, Nov. 12, 1933, *R. A. Darrow 498;* PARATYPE: Santa Catalina Mts., on soil, 8000 ft., Nov. 12, 1933, *Darrow 503.*

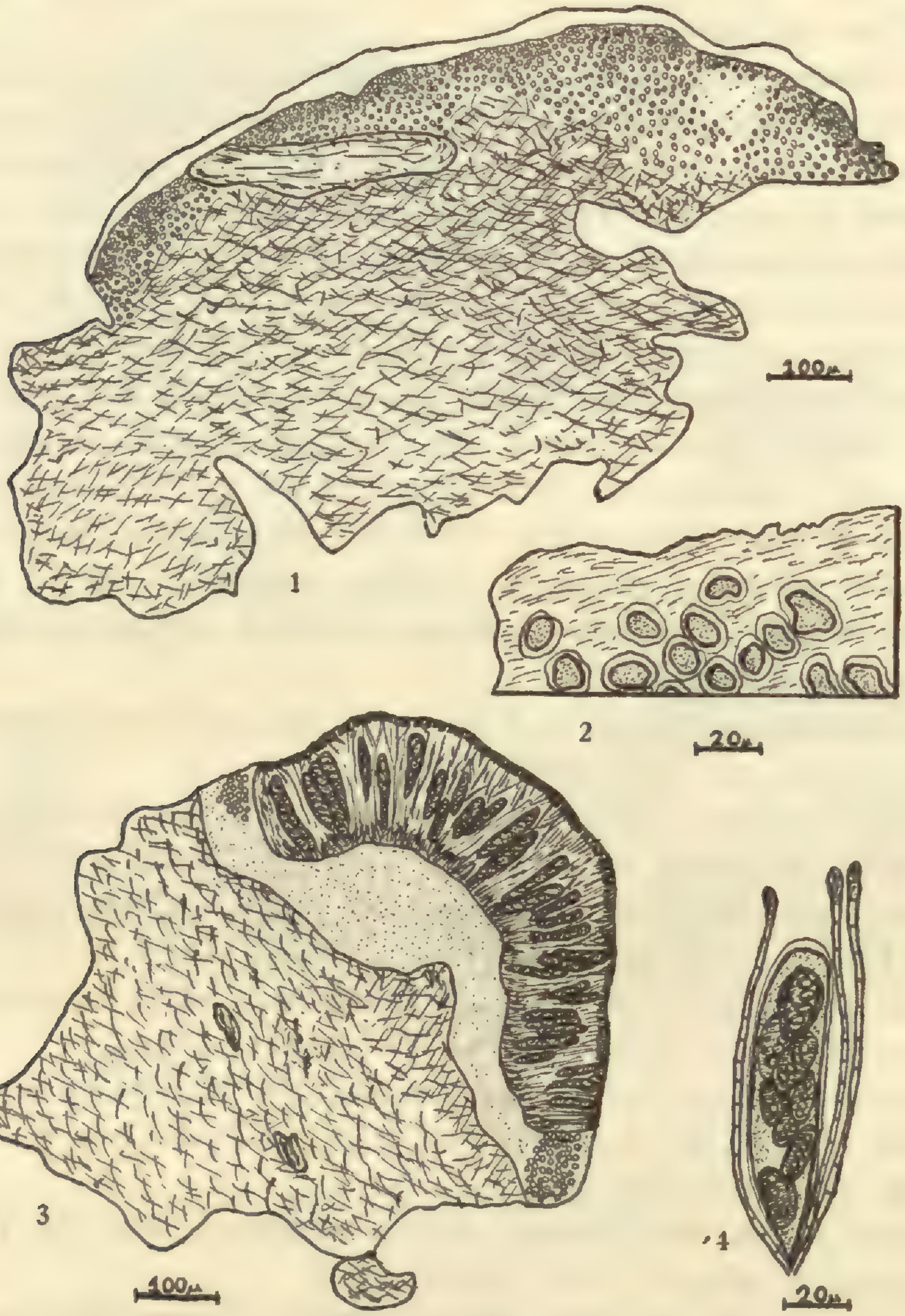


Fig. 3. *Rinodina darrovii* E. Rud.

1. Section of thallus.
2. Enlarged section showing cortex.
3. Section of an apothecium.
4. Ascus with associated paraphyses.

Thallus ochraceus vel cinnabarinus, granulosus, K—, diffractus; cortex gelifactus, erodus; algae protococcoideae, cellulis sphaericis vel angulosis, 5–10 μ diametro, in strato continuo 57–71 μ crassitudine sub cortice; medulla densa, hyphis indistinctis circa 1.5 μ diametro intertextis. Apothecia nigra, 0.5–1.0 mm. diametro, plana vel convexa; margine thalloideo, tenui, mox emarginato, thallo concolore; hypothecium hyalinum, in centro 80 μ altitudine; thecium 27–34 μ altitudine; paraphyses 2 μ diametro, septatae, simplices; asci 70–71 $\times$ 10–16 μ, clavati; sporae 8-nae, biseriatae, 17.4–24.4 $\times$ 8.7–11.5 μ, primo non-septatae, deinde tri-septatae, brunneae.

Thallus ochraceous-tawny to cinnamon-brown, granulose, broken in places into irregular pieces, KOH—; cortex gelatinous, eroded in parts; algae protococcoid, forming a continuous layer 57–71 μ thick, the cells spherical to angular, 5–10 μ in diameter; medulla of tightly woven, indistinct hyphae about 1.5 μ in diameter. Apothecia black, 0.5–1.0 mm. in diameter; disc flat to convex; margin thalloid, thin, of same color as the thallus, soon disappearing; hypothecium hyaline, of closely woven hyphae, about 80 μ thick at center; thecium 27–34 μ high; paraphyses filiform, septate, about 2 μ thick, swollen at tips and incrusted with yellow crystals, unbranched; asci clavate, 70–71 $\times$ 10–16 μ; spores 8, biseriate, brown, at first 1-celled becoming 4-celled, 17.4–24.4 $\times$ 8.7–11.5 μ.

This species has the general appearance of *Rinodina phaeocarpa* (Sommerf.) Vainio (*R. nimbosa* (E. Fr.) T. Fr.) but the four-celled spore places it in the subsection CONRADIA Malme as recognized by Zahlbruckner (1926). Its affinities seem to be with *R. conradi* Koerb. from which it can be separated by its larger black apothecia, its indistinct cortical hyphae, and its thicker hypothecium. The spores in this species have not been found to have more than four cells and also to be slightly smaller than those of *R. conradi.*

RINODINA EURYSPORA Zahlbr.—ARIZONA: Santa Rita Mts., on igneous rock, 7000 ft., Aug. 14, 1934, *Darrow 821.*

RINODINA NOVOMEXICANA B. de Lesd.—ARIZONA: Santa Rita Mts., on igneous rock, 4500 ft., June 3, 1934, *Darrow 707;* 7000 ft., Aug. 14, 1934, *Darrow 823.*

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THE ANALYSIS OF SUSPECTED HYBRIDS, AS ILLUSTRATED BY *BERBERIS* × *GLADWYNENSIS*

EDGAR ANDERSON

During the last fifteen years a considerable portion of my time has been spent in attempting to measure the importance of hybridization in the evolution of natural populations. More than a score of genera have been studied intensively in the wild (and whenever feasible in the breeding plot as well) with students and associates, though as yet only a fraction of these studies has been published. Various techniques have been worked out for dealing with such problems (Anderson, 1949, chap. 6), and as their validity has been more widely recognized (Stebbins, 1952) they are being more widely adopted. In the course of helping workers elsewhere to adapt these methods to their own problems I have become increasingly aware that in part they are based upon a scrutiny of the original material more exhaustive than is customary in many laboratories. It has accordingly seemed expedient to describe the procedure in more elementary detail than hitherto. Instead of discussing the complexities of hybridization in natural populations I have chosen the relatively simple example of an apparent hybrid which arose spontaneously in the garden of Mrs. J. Norman Henry, of Gladwyne, Pennsylvania. This seems a particularly happy choice since it also serves to demonstrate the usefulness of these methods in dealing with horticultural material of unknown ancestry.

A vigorous young barberry was found coming up in the shelter of a large bush of *Berberis verruculosa* in Mrs. Henry's garden. *Berberis verruculosa* is a dense, evergreen-leaved plant, certainly the most distinctive of the hardy barberries. The seedling, so obviously related that it must have been a seedling of *B. verruculosa*, was nevertheless so different from it that Mrs. Henry had supposed it was probably a spontaneous hybrid. It was different from any barberry known to her or to me and it exhibited the hybrid vigor which is the mark of so many hybrids. Furthermore, many garden hybrids of *Berberis* are known and Mrs. Henry at various times had grown a number of other species of *Berberis* in her garden. With her permission a precise examination was made both of the putative hybrid and of *Berberis verruculosa* to establish the probable ancestry.

The following is the procedure established in this laboratory for such examinations:

1. Choose comparable material of parent and hybrid.

2. Examine, describe, and measure each feature item by item. Use great care to work with truly comparable material. Do not attempt comparisons of a branch grown in the shade from one specimen and one grown in the sun from the other. If one is from a fruiting branch, then the other should be also. Use great care in distinguishing between long shoots and short shoots. Many plants without such conspicuously heterogeneous shoot systems as the *Ginkgo* have a more or less well-defined short shoot-long shoot system which requires careful examination to perceive.

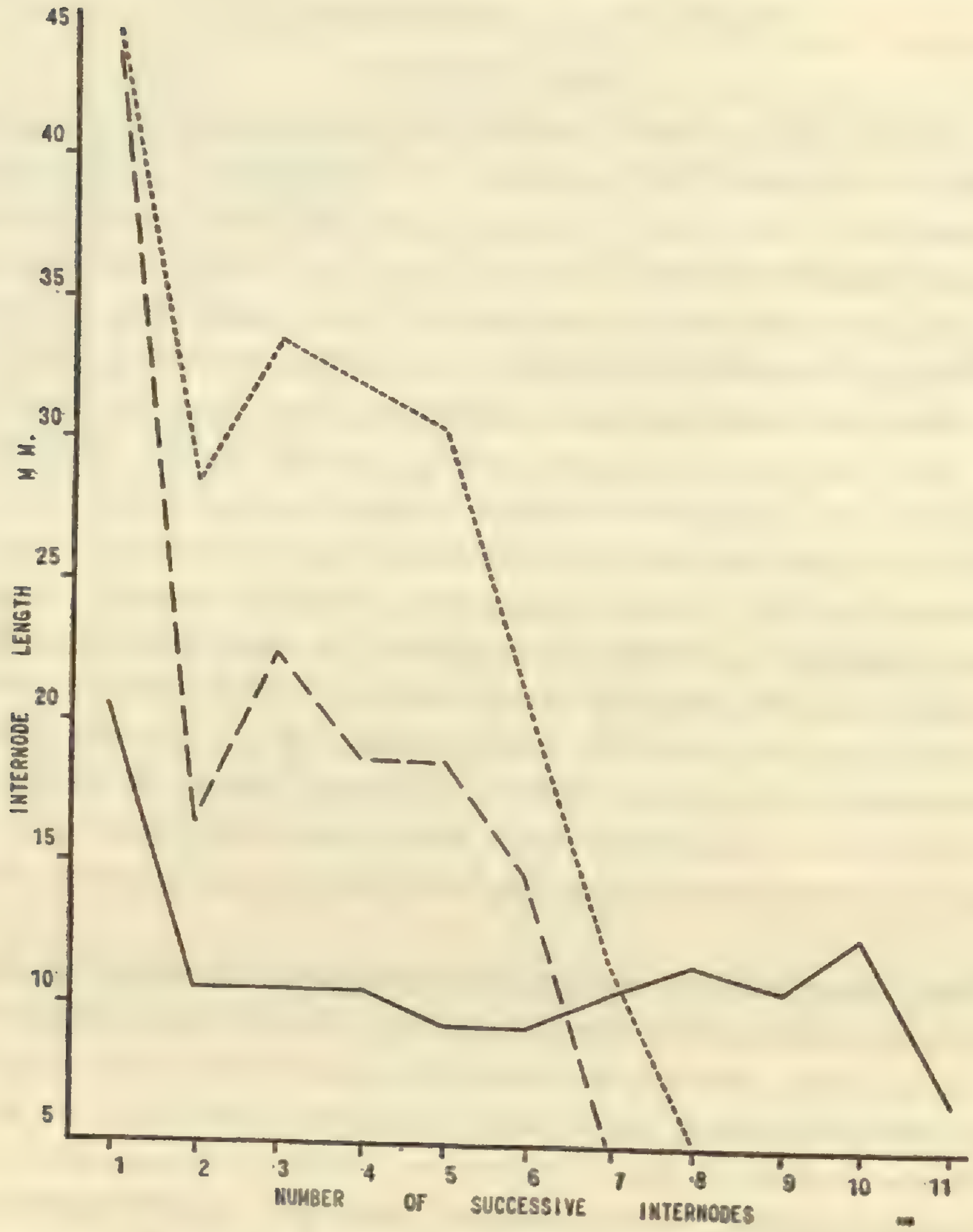

Fig. 1. Internode diagrams of comparable branchlets of two species of barberry and their putative hybrid. Solid line, *Berberis verruculosa;* long dashes, *Berberis* × *gladwynensis;* short dashes, *Berberis Julianae.* As explained in Anderson and Schregardus (1944), these diagrams are made by plotting the lengths of successive internodes from the base to the tip and connecting these points with an imaginary line. The first internode at the base of the branchlet in *B. Julianae,* for instance, is 45 mm. long, the second is 28 mm., the third, 33 mm., etc.

3. (And, most important): Conduct the entire examination, if possible, against a plain neutral background. Cover the table top with clean wrapping paper or some such material. Remove all distracting objects such as pencils, paper clips, erasers, etc., out of the immediate field of vision. The eye can work much more efficiently in the perception of resemblances and differences if it can concentrate upon the problem in hand. Work in a good light and have a good dissecting microscope. Choose a series of comparable branches and lay them out side by side with equal spacing. Choose a series of comparable leaves and lay them out side by side in the same manner, with their apices all pointing in the same direction. These seem like points much too elementary for serious scientific dis-

cussion, and yet in assisting other people to use my methods I nearly always find that these precautions have not been followed and that it is difficult to convince other scholars of their supreme importance. This is one of those ridiculously simple matters which are far more important than they seem and which are indicative of true scientific precision. Specific differences are frequently subtle and they can be apprehended much more readily if one uses comparable material, a neutral background, and a good light.

4. Make measurements with good steel calipers and a steel metric rule.

5. Pay particular attention to pubescence, pubescence pattern, internode pattern (Anderson and Schregardus, 1944), branching pattern. Careful analysis will show that nearly all closely related species of the higher plants differ significantly (and with enough study, definably) in their internode patterns.

Comparable branches were accordingly chosen from *Berberis verruculosa* and the seedling. Both were selected from well-developed branches of flowering age, growing in almost full sun and borne upon the upper parts of their respective plants. After these two branches had been examined carefully against a neutral background, comparable branchlets were chosen for further study as follows: Proceeding from the tip, the first strong secondary branch (all of the current season's growth) was selected for study. The internode lengths of this branchlet were measured to the nearest millimeter, the results being plotted as an internode diagram (fig. 1).

Hybrids are usually intermediate between their two parents when due allowances are made for heterosis, for growth-pattern differences, and for possible differences in ploidy. From a study of fig. 1, it is possible to make several predictions as to the putative male parent of the seedling barberry. *B. verruculosa* is shown to have more and shorter internodes than the seedling. Its basal internode is only about twice as long as the other internodes and the remaining internodes are subequal. The seedling has a basal internode more than twice as long as the others and the remaining internodes are not at all uniform in length and seem to have a definite pattern of decreasing length toward the tip. We therefore predict that the putative parent (when comparable material is studied) should have conspicuously non-uniform internode lengths with a very long internode at the base of such branches and decreasingly short ones as the tip is approached, probably in a well-defined pattern.

Leaf comparisons were then made. Choosing comparable leaves proved to be difficult but not impossible. Leaf size and shape were uniform in *B. verruculosa* but variable in the seedling. Care had to be taken, therefore, to choose exactly comparable material. Most of the primary leaves in these barberries are spines. The leafy leaves are borne on short secondary branches in the axils of the spine-leaves, giving the appearance of little clusters up and down the branches. In *B. verruculosa* all the leaves on the plant were superficially similar in size, shape, and serration. In the seedling they differed markedly. Those in clusters arising from the older wood were variable. Among them were leaves which were narrower

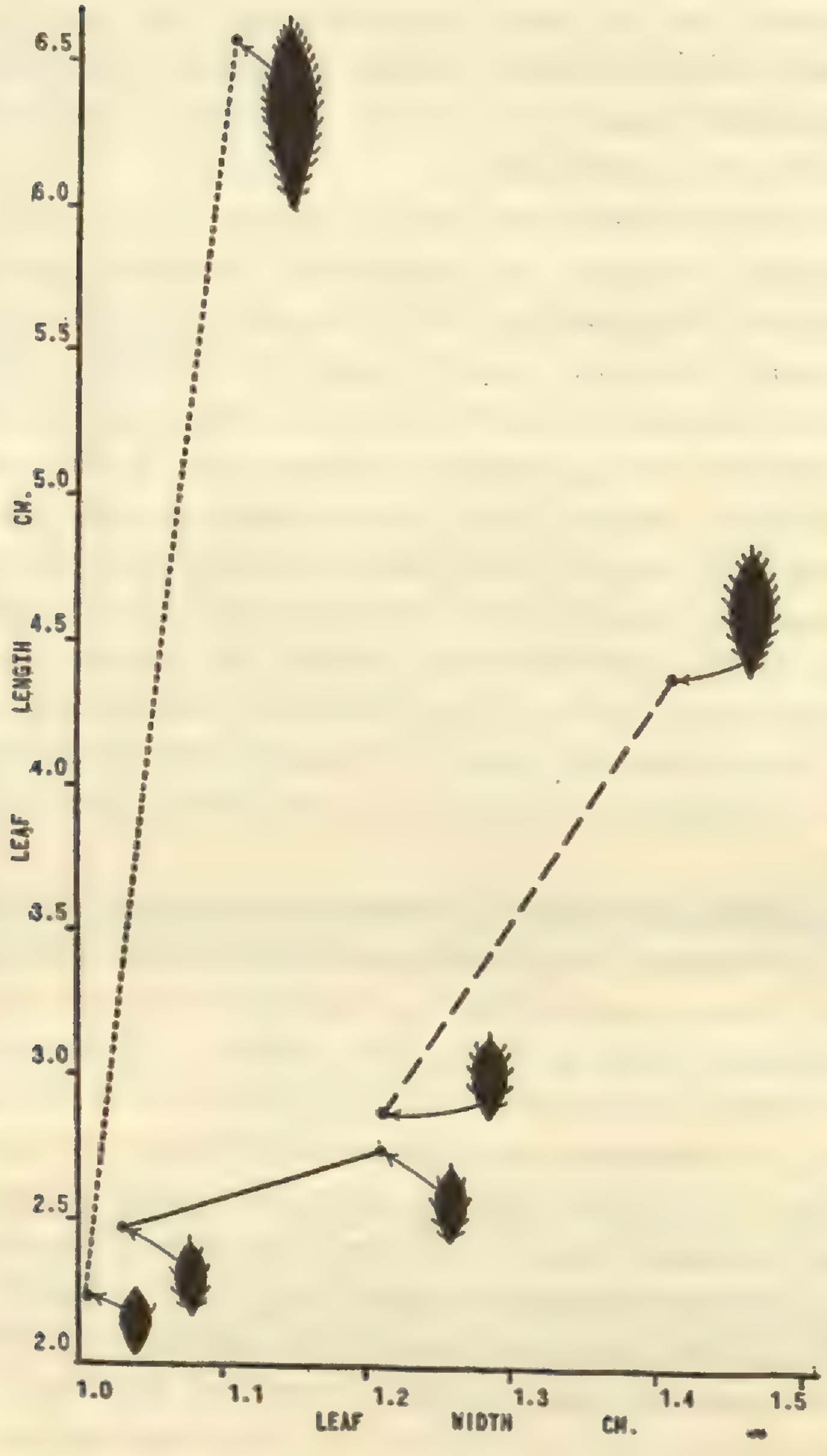

Fig. 2. Relationships of size, shape, and number of marginal setae in leaves from young and mature spurs for two species of barberry and their putative hybrid. As in the previous figure, a solid line indicates *B. verruculosa*, short dashes, *B. Julianae*, and long dashes, *Berberis* × *gladwynensis*, their putative hybrid. The figure shows simultaneously the length, width, and seta number of comparable leaves from young and from old spurs; the slope of the lines also indicates the change in shape from young to old: *Berberis Julianae* changes conspicuously in size, shape and seta number from young to old spurs; *B. verruculosa* scarcely at all; their hybrid is intermediate in degree of change. The silhouettes of leaf size and shape appended to the diagrams, while highly diagrammatic, are all to the same scale and represent average values from actual measurements.

in shape, larger in size and with more strongly developed setae at the tips of the serrations along their edges. Careful examination then showed that *B. verruculosa* had a very slight tendency in the same direction though not strong enough to be readily apparent without examination. Measurements showed that while *Berberis verruculosa* and the seedling had about the same number of setae per leaf on the new wood, the seedling had nearly twice as many as *verruculosa* on the old wood. Figure 2 shows all these relationships. The putative parent for which we are searching should have leaves on its new wood as small as those of *verruculosa*, or even smaller, with greatly differentiated leaves on the older wood. Some of the leaves on the older wood should be very long, proportionately narrow, and with many setae along their edges.

As, in this fashion, one proceeds feature by feature in the careful comparison of the one parent with the hybrid, he becomes progressively better acquainted with the general ground plan of the plant and is increasingly capable of making precise comparisons and valid inferences. Before long it is possible to draw up precise descriptions not only of *B. verruculosa* and its hybrid seedling but also of the putative male parent. Such a comparison is presented below in tabular form, including the predictions as to the male parent.

verruculosa	*gladwynensis*	unknown *(Julianae)*
Branches arching, sub-horizontal	Branches sub-arching, some nearly erect	Branches straight, erect to horizontal
Internodes short, uniform	Internodes medium, variable	Internodes long, very variable
Branchlets densely glandular	Branchlets at most sub-glandular	Branchlets eglandular
New growth scarcely differentiated	New growth clearly differentiated	New growth strongly differentiated
Mature bark barely ribbed	Mature bark definitely ribbed	Mature bark strongly ribbed and furrowed
Wood greenish	Wood yellowish-green	Wood bright yellow-green
Spines up to 1.2 cm.	Spines up to 1.3 cm.	Spines up to 1.5 cm.
Leaves glossy, dark green above, glaucous below	Leaves somewhat glossy, medium-dark above, sub-glaucous below	Leaves not glossy, bright green above, light green below
Fall color a more or less general purple	Fall color stronger on newest growth, occasional colored leaves	Brilliant fall color
Leaves on new and old growth scarcely differentiated	Leaves on new and old growth definitely differentiated	Leaves on new and old growth strongly differentiated
Largest leaves on old spurs 27 mm. × 12 mm.	Largest leaves on old spurs 43 mm. × 14 mm.	Largest leaves on old spurs 65 mm. × 11 mm.
10 marginal setae at most	20 marginal setae at most	Over 30 marginal setae
Flowers borne singly or in pairs	Flowers in fascicles of 5 to 8	Flowers in fascicles of 15 to 25
Stigma sessile	Stigma sub-sessile	Stigma definitely not sessile, style of at least 1 mm.

As the description began to resolve itself my knowledge of barberries was sufficient to suggest that *Berberis Julianae* was probably the barberry we were looking for. As soon as I made this suggestion Mrs. Henry informed me that a large bush of this species had once stood just a few feet away from *B. verruculosa* but it had been damaged in a windstorm and removed. Many of the technical points in the description, however, involved matters which were completely outside my knowledge of barberries. Predictions as to the numbers of setae on the mature leaves, the number of flowers per fascicle, the presence of a style, etc., were drawn up with no knowledge of what they might be like in *B. Julianae.* The entire hypothetical description was then run down in Rehder's key (Rehder, 1940) to the barberries just as if one had the specimen actually in his hand. It led to *B. Julianae* and fitted the description of that species precisely, down to the most technical detail.

There can be little doubt, therefore, that the seedling was a spontaneous hybrid, *B. verruculosa* × *B. Julianae.* I am accordingly describing it as:

Berberis × **gladwynensis** hyb. nov.[1] Intermediate between its parents *B. verruculosa* and *B. Julianae.* Flowers in fascicles of 5 to 8, stigma subsessile, leaves subglaucous below, nearly evergreen. Type: *Henry,* in the herbarium of the Philadelphia Academy of Natural Sciences; from the type bush, *E. Anderson s. n.,* MBG.

It is a pleasure to name this handsome barberry after the site of Mrs. Henry's garden which has long been a mecca to botanists and gardeners alike.

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[1] Berberis **gladwynensis** hyb. nov. inter parentes *B. verruculosam* et *B. Julianam.* Flores in fasciculis 5–8, stigmate subsessile. Folia fere semperviridia, subter subglauca.

VARIATION IN COB MORPHOLOGY AMONG CERTAIN ARCHAEOLOGICAL AND ETHNOLOGICAL RACES OF MAIZE

NORTON H. NICKERSON*

Introduction

Zea Mays L., one of the most highly evolved of all grasses, is still botanically much of an enigma. Commonly known as Indian corn or maize, it was a very important plant to the peoples of the New World long before the arrival of Columbus. It formed the basis of the highly developed Inca, Maya, and Aztec civilizations and was the staple crop from Canada to Chile for several thousand years. It is, of course, quite important to the present-day inhabitants of Central and South America, and agriculture and industry in the United States uses three and one-quarter billion bushels annually.

Botanists have until recently followed almost exclusively Sturtevant's (1899) classification of contemporary races of maize by kernel types. Although this classification is an artificial one, it has proven to be of practical commercial worth. Archaeologists have long known the value of maize kernels found at excavation sites for determining types of maize grown and the uses to which they were put. Until the last few years, other parts of the maize plant have been quite generally neglected as a source of historical data, chiefly because of the complexities involved in determining and evaluating such evidence as they contain. Evidence from maize tassels has been used with promising results (Alava, 1952; Anderson, 1944b, 1944c, 1949a, 1951; Anderson and Brown, 1948; Anderson and Cutler, 1942; Brown *et al*, 1952; Cutler, 1946; Wellhausen *et al*, 1951, 1952). Prat (1948) showed that in maize and other grasses hairs and other epidermal emergences can be used as a basis for identification and classification. Internode patterns have been studied by several workers (Anderson, 1943, 1949a; Anderson and Brown, 1948; Anderson and Schregardus, 1944; Stonor and Anderson, 1949; Wellhausen *et al*, 1951, 1952). Ear and tassel ontogeny have been studied by Bonnett (1940, 1948) and Kiesselbach (1949). Esau studied the ontogeny of the maize vascular bundle.

Surprisingly little has been done to measure and evaluate those morphological structures which are present on a maize cob after the kernels have been removed. Weatherwax, a pioneer in the study of the maize cob, pointed out (1918) the need and value of accurate morphology in understanding this structure, and demonstrated (1920) the orderly spikelet behavior underlying changes in kernel rowing. Fujita (1939) observed that an even number of pairs of kernels resulted in straight rows, and an odd number in spiral rows. Cutler (unpublished work) made many histological studies of the cobs of both North and South American maize, as well as of several closely related genera. Lenz (1948) indicated the types

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The stimulating advice of Dr. Edgar Anderson and the technical assistance of Mr. Ding Hou throughout the course of this investigation are hereby gratefully acknowledged.

of evidence available from a histological study of the maize cob. Alava (unpublished work) modeled in great detail small portions of the exterior surface of a maize cob. Mangelsdorf and Smith (1949) tabulated a number of external and internal maize ear characters, and their general procedure was used in characterizing 25 present-day races of maize in Mexico by Wellhausen *et al* (1951, 1952). These studies were based on the evaluation of many characters which did not involve exact measurements. In the present study, the value of several morphological characters used by these investigators has been increased by employing exact measurements. Other measureable morphological characters have been found which are of significance in tracing historical influences of one race of maize upon another.

There are two reasons why evidence present on the maize cob is important. The first one is based on the generally accepted fact that distinguishing characters are not distributed at random among plants; with regard to their occurrence in the Maydeae, agrostologists have found the female inflorescence to be of particular significance. The second reason, already pointed out by Lenz (1948), is that there are more archaeological remains of maize cobs than of any other plant material. The importance of these remains can perhaps be appreciated when one considers that maize, unlike most cultivated crops, is completely dependent upon man for its preservation. This fact can only mean that it has had a constant association with man since its adoption as a food plant, and that in its manner of origin, in the course of its migrations, in its development into a myriad of races, and in its intimate association with ancient religious symbolism, the history of maize becomes intimately tied to the history of man. Increased insight into the one will certainly add to our present understanding of the other.

For a reasonably complete investigation of the maize cob, the following three courses were deemed necessary: (1) to measure certain easily-recognized features of the maize cob and to interpret their morphological nature; (2) to set forth one possible scheme of analysis of the variation patterns of different races of maize based on these measurements; (3) to discuss the resulting indicated trends as to their validity and applicability in extending our present understanding of the history of maize.

Morphology of the Ear

Bearing in mind that an adequate treatment of variation in maize ears would be more complete if the nature of those parts under discussion were understood, a detailed study of morphological structures found on the maize ear was first undertaken. However, since the results are of a technical nature quite different from those obtained from a study of variation, they are treated elsewhere (Nickerson, in press).

MORPHOLOGICAL STRUCTURES EXAMINED

One of the purposes of this study in variation is to determine what morphological structures expressed in the cob are of significance in differentiating between races of maize. To accomplish this, several characters had to be included which ultimately proved to be of little use. A total of 526 cobs was examined for each of the three external and five internal characters discussed below.

EXTERNAL CHARACTERS

Shape of Ear.—This character is the only one used in the investigations which is dependent upon a subjective grading. Ears were classified into one of four types: straight, cigar-shaped, tapered, enlarged butt. Two of these types—straight and tapered—were used in analysis of each sample. For reasons discussed elsewhere (Nickerson, in press), a straight-eared race exhibits less condensation than a tapered- or enlarged butt-eared race, and a race with cigar-shaped ears is intermediate between these extremes.

Shank Diameter.—The diameter of the shank was measured in millimeters at a point close to the base of the ear, above the last apparent husk node whenever possible. In specimens with elliptical shanks, two measurements were made and an average of these was used. Shank diameters are fairly consistent within any one kind of maize and are often markedly divergent between different kinds.

Row Number.—Row number was determined by counting the number of vertical rows of glumes in the middle area of the cob. The middle area was used for this and all subsequent measurements because of its uniformity of size, stage of development, and freedom from growth irregularities common at both base and tip of the ear. Row number is a readily-observed character the importance of which is not yet fully understood. Anderson and Brown (1948) were able to correlate the condensation index of the tassel with kernel row number in the ear. Cutler (1952) used row number in his preliminary study of cobs from successive layers of cultural remains found in Tularosa Cave. His tables indicated the presence of high row numbers in lower strata and progressively lower row numbers in successively higher strata. These data show the reverse of the situation reported for the stratified remains of Bat Cave by Mangelsdorf and Smith (1949), who stated that in general the older (and more pod-corn-like) the ear, the lower was its row number.

INTERNAL CHARACTERS

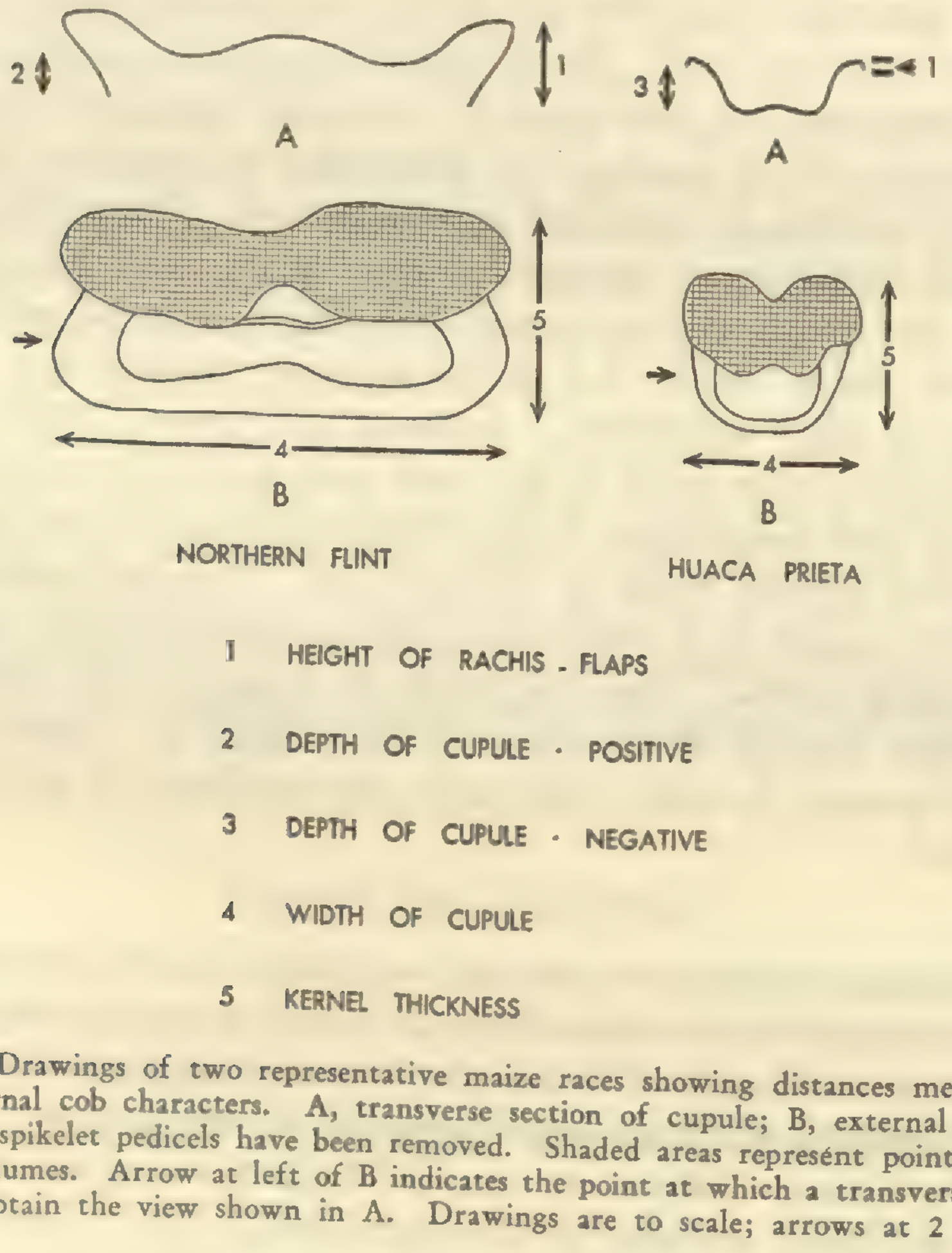
To study internal characters, the ear was broken in two at the approximate middle; the exposed ends were then observed under a dissecting microscope.

Width of Lower Glume.—This character was measured in millimeters with the calipers held perpendicular to the widest point on the abaxial surface of the glume. The measurement is not a direct expression of a particular gene such as Mangelsdorf and Smith (1949) reported for the relationship between lower glume length and various alleles of the *Tu* gene, but reflects the width of the basal portion of the kernel which it encloses.

Height of Rachis-flaps.—This measurement in millimeters was made perpendicular to the axis of the cob. In instances where the rachis-flaps were of unequal height, an average measurement was used. The rachis-flap is a part of the cupule (Nickerson, in press) and its significance is somewhat minimized by its variability in some otherwse homogeneous samples used in the present investigation. Mangelsdorf and Smith (1949) reported the same situation for maize cobs from Bat Cave, but Wellhausen *et al* (1951, 1952) found rachis-flaps to be extremely useful in characterizing races of maize in Mexico.

Depth of Cupule.—This measurement in millimeters was made perpendicular to the cob axis, and was given a positive or a negative value, depending upon whether it was out from, or down into the rachis. It represents the extent of adnation of the cupule-forming prophyll (Nickerson, in press) to the axis, and is well correlated with ear shape.

Width of Cupule.—This measurement was made by holding the calipers at right angles to the cob surface and measuring the distance in millimeters between



Text-fig. 1. Drawings of two representative maize races showing distances measured in determining four internal cob characters. A, transverse section of cupule; B, external view of cupule after glumes and spikelet pedicels have been removed. Shaded areas represent points of attachment of spikelets and glumes. Arrow at left of B indicates the point at which a transverse cut was made in each case to obtain the view shown in A. Drawings are to scale; arrows at 2 and 3 are each 1 mm. long.

any pair of outside rachis-flap edges across their cupule. It is in part an indication of kernel width, in that wide cupules always mean wide kernels.

Thickness of Kernel.—The distance along the cob axis from the base of one set of lower glumes to the upper edge of their cupule is exactly equivalent to the thickness of each kernel produced there. The measurement is useful in making comparisons between productivity of different cob samples, especially those involving fragmentary archaeological remains.

These last four characters were recorded in outline drawings carefully made to scale (working with calipers under a dissecting microscope) for each of the 526 cobs examined (text-fig. 1). Other characters measured but not used include height and texture of the lower glume and longitudinal profile drawings of each cupule. Diameters of the pith, cob, and rachis were measured and the cob/rachis index (Mangelsdorf and Smith, 1949), as well as the rachis/pith index, was computed for all specimens. However, neither the averages nor the individual variations of these indices were found to be particularly characteristic among the maize samples studied in this investigation.

Names, Sources, and Anthropological Background of Samples

Maize samples examined were of diverse origin both geographically and temporally. Races of contemporary maize here included were chosen as typical for those parts of the world. Archaeological cob samples were largely from the southwestern United States, but included one sample from Lower California and two extensive collections from sites excavated by Junius Bird in Peru and northern Chile. In listing the samples they are grouped arbitrarily into geographical units; no further inferences should be drawn from this arrangement. Samples, except where otherwise noted, are from the maize collection of the Museum of Economic Botany of the Missouri Botanical Garden, St. Louis.

NORTH AMERICA

Present-day Races:

Iroquois Sacred Flour.—This sample was from material originally grown by Professor Frank P. Bussell from seed collected by Erl Bates from the Iroquois Indian tribes of northern New York. The Indians grew it under conditions of strict isolation for ceremonial use (Anderson, 1947b). Ears are straight, 20–28 cm. long, with heavy shanks and 8 rows of wide white or yellow (sometimes pale blue) kernels. Fourteen ears were examined.

Northern Flint.—A composite sample, this group included flint corns from the Northeast (Parker's, Canada, Mammoth Yellow, Longfellow) and the upper Great Plains (Winnebago, Bear Island, Brownell, Mandan, Tama, Golden Chippewa). Brown and Anderson (1947) studied these and other representative flint varieties and reported that the ears were long and slender with 8–10 rows of wide, crescent-shaped kernels, heavy shanks, and a tendency toward a large cob base. Twenty-three ears were examined.

Hopi White Flour.—This sample was furnished by Dr. William L. Brown, Pioneer Hi-Bred Corn Co., Johnston, Iowa, who collected it at the Hopi town of Hotevilla, Arizona. Carter and Anderson (1945) considered Hopi White Flour to be an example of Puebloan maize. Brown *et al* (1952) reported that this variety is one of their main sources of meal. The straight ears are 18–24 cm. long, with wide shanks, no basal compression, and wide white kernels in 12–14 rows. Seven ears were examined.

Hopi Blue Flour.—Also furnished by Dr. William L. Brown, this collection has substantially the same history as Hopi White Flour. However, Brown *et al* (1952) reported that it is probably more important as a source of food. The cigar-shaped ears are 14–20 cm. long, with small shanks, a tendency toward basal compression, and 10–20 rows of narrow blue-aleuroned kernels with white endosperm. Eleven ears were examined.

Papago Flour.—This race of maize is grown by the desert-dwelling Papago Indians, and was reported by Carter and Anderson (1945) to be quite similar to prehistoric Basketmaker maize. The ground kernels make a meal of excellent quality. Ears are 20–25 cm. long, cigar-shaped, with narrow shanks and 12–14 rows of isodiametric yellow kernels with white endosperm. Twenty-five ears were examined.

ARCHAEOLOGICAL REMAINS:

Basketmaker.—Cobs included in this collection were recovered from Kinboko and White Dog Caves, both of which are located in Tsegi Canyon, Marsh Pass, northeastern Arizona. The samples were submitted by Mr. Harold S. Gladwin, who estimated their age to be *circa* 200–300 A.D. On the basis of there being no pottery associated with these cobs, they are believed to belong to the cultural level known as Basketmaker II. The cigar-shaped cobs are 6–12 cm. long, and bore somewhat isodiametric kernels in an average row number of 14. Six cobs were examined.

Marsh Pass.—Cobs included in this collection were recovered in West Hackberry Canyon and Turkey Cave, both of which are located in Tsegi Canyon, Marsh Pass, northeastern Arizona. These samples were also submitted by Mr. H. S. Gladwin, who estimated their age to be from 300 A.D. to about 1000 A.D. The collection represents cultural levels from late Basketmaker II or later up through Pueblo II. The predominantly cigar-shaped cobs are 6–14 cm. long, and bore kernels wider than thick in an average row number of 10. Thirty-one cobs were examined.

Turner Site.—This sample consisted of 50 cobs and fragments recovered from the Turner Site, near Cisco, Utah, by H. M. Wormington, Curator of Archaeology, Denver Museum of Natural History. Wormington estimates its age to be around 1000 A.D. (personal communication, 1953), and believes that the site was inhabited by peoples who were culturally a later manifestation of the Fremont Basketmakers. Remains of their culture were recovered from Castle Park in the

Yampa River Valley, Utah, and are dated at 400–800 A.D. by Burgh and Scoggin (1948). There are nearly equal numbers of tapered and cigar-shaped cobs in this collection; some were not used in this study because of their fragmentary nature. Cobs are short, 3–8 cm. long, charred, with medium shank diameters and medium-wide kernels in an average number of 12 rows. Twenty-seven cobs were examined.

Luster Cave.—Ten cobs were recovered by Dr. Robert Lister, Department of Anthropology, University of Colorado, Boulder, from a cave located in Utah, just west of the Colorado state line, in the Glade Park area. A preliminary report (Lister and Dick, 1952) described the archaeological finds of this cave and of other nearby sites. On the basis of pottery types, the maximum possible age assigned to Luster Cave by these workers is 900–1000 A.D., but it may be much more recent. The straight and tapered cobs are generally uncharred and fairly complete with small shank diameters and wide kernels in an average number of 10 rows. Nine cobs were examined.

Tularosa Cave.—More than 30,000 maize cobs were recovered from this site in Pine Lawn Valley, northeast New Mexico, by archaeologists from the Chicago Natural History Museum. The Museum has submitted these cobs to Dr. Hugh C. Cutler, who has generously made available for inclusion in the present study samples representing three levels of Square 3R2. Maize cobs from the lowest levels of Tularosa Cave were dated at 2300 ± 200 years by the Carbon 14 method. The cave is estimated to have been abandoned somewhere around 1000–1200 A.D., and thus was continuously occupied for about 1500 ± 500 years (Martin *et al*, 1952). Material from Square 3R2, Levels 3, 6, and 11 was studied as three separate samples, each of which was chosen so that the cobs analyzed reflected the proportionate row numbers determined by Cutler (1952) from all cobs found in each of these layers. There was a decrease in row number from the lower levels to the surface, average row numbers for Level 11 being 12–14, for Level 6, 10–12, and for Level 3, 8–10. Culturally, Level 11 is the oldest (400 B.C. ± 200 years) and represents the Pre-pottery Phase. Level 6 dates back to 500–600 A.D., and represents the Georgetown Phase. Level 3, at 1000–1200 A.D., represents the San Francisco Phase. Twenty-five cobs from each of the three levels were examined.

Point of Pines.—This sample consists of about 250 ears of charred maize. It was recovered from Room 50 of a large ruin at Point of Pines, Arizona, numbered Ariz. W:10:50, and was submitted by Dr. Emil W. Haury, Director, Arizona State Museum, Tucson, Arizona. He believes its age to be 1250 A.D. (personal communication, 1953). It can be assigned to the Pueblo II cultural phase. The straight and cigar-shaped ears are 5–8 cm. in length, with small shanks and smooth kernels wider than thick in an average number of 10 rows. Seventy-five cobs were examined.

MEXICO AND CENTRAL AMERICA

PRESENT-DAY RACES:

Chapalote.—This race of popcorn is considered by Wellhausen *et al* (1951, 1952) to be one of the ancient indigenous races of Mexico. It was mentioned by Anderson (1944a, 1946) as being allied to the primitive *Maíz reventador.* Wellhausen *et al* pointed out its resemblance to archaeological maize finds at Painted Cave (Haury, 1945) and Cottonwood Cave (Hurst, 1948; Hurst and Anderson, 1949). They considered it to be one of the most distinctive races of maize in Mexico. Mangelsdorf (1948) and Mangelsdorf and Smith (1949) regarded it as possessing the "weak" allele for pod corn. The cigar-shaped ears are 10–15 cm. long, with small shanks and smooth rounded chocolate-brown kernels in an average row number of 12. Ten ears were examined.

Guatemala Flint.—A common variety of the Guatemala highlands, this race was described by Anderson (1947a), who considered it to represent one of the basic elements in Guatemalan maize. Ears are 10–25 cm. long, with a conspicuously enlarged and irregularly rowed butt, heavy shanks, a heavily sclerenchymatized rachis, and wide flinty kernels (some of which are capped with soft starch) in 8 (occasionally 10 or 12) straight rows. Eleven ears were examined.

ARCHAEOLOGICAL REMAINS:

Lower California.—This sample of 52 maize remains was recovered from Cave B. C. 100, located 8–10 miles east-southeast of Comondu, in central Baja California, and was submitted by Dr. William C. Massey, Dept. of Anthropology, University of Washington, Seattle. The cobs were recovered from a layer dated by Dr. Massey at 1697–1750 A.D. (personal communication, 1953). The cigar-shaped and straight cobs are 6–12 cm. long, with small shanks, and bore nearly isodiametric kernels set in 10–12 rows. Thirty-five cobs were examined.

SOUTH AMERICA

PRESENT-DAY RACES:

Peru Flour.—This sample was collected by G. Edward Nicholson at Huancayo, Peru, where it was being offered for sale in one of the native markets under the name of "*Maíz de Color.*" It belongs to the race Cutler (1946) called "Valle Maize." Ears are short, tapering, constricted at the base, with small shanks. The race exhibits little sclerenchymatization. Kernel color varies from ear to ear; brown, red, yellow, and various delicate striped combinations are most common. Kernels are pointed, as wide as thick, and arranged in prominent rows averaging 10 per ear. Twenty-three ears were examined.

Coroico.—This race, described by Cutler (1946) as "the most unusual race so far known," has the odd characteristic of brick-like arrangement of "alicoles" (cupule plus pair of associated spikelets; Nickerson, in press). Cutler described the tapered ears as long, slender, and flexible (25–30 cm. lengths were common in the collection examined), with a light brown cob, small pith, and brown-orange

kernels. He stated that the row number averaged 9, but he now believes (personal interview, 1953) that two successive rings of alicoles constitute a single diametral whorl; thus the row number of Coroico is generally high, averaging 18. Whether 9 or 18 rows are present is governed by the state of condensation of the cob axis. Twenty-five ears were examined.

ARCHAEOLOGICAL REMAINS:

Arica.—These samples were recovered from two midden sites, Playa Miller and Quiani, located on the coast in the vicinity of Arica, Chile (18° 30′ S. Latitude), by Junius B. Bird, Associate Curator of Archaeology, American Museum of Natural History, New York. Cobs from both sites were treated as one sample following Bird's (1943, 1948) suggestion that Playa Miller represented a continuation of sequences started at Quiani. The oldest maize remains from this area are dated at about the time of Christ (Bird, personal communication, 1952). It is thus younger than material from the Huaca Prieta sites discussed below. The cigar-shaped and tapering cobs are 5–12 cm. in length and 1–2.5 cm. in width, with small shanks and an average row number of 14. Twenty-one cobs were examined.

Huaca Prieta.—These samples, also from the American Museum, were recovered by Junius B. Bird from Huaca Prieta, a site on the Peruvian coast at the south of the Chicama Valley (app. 8° S. Latitude). These comprehensive samples consist of 604 cobs from Test 1 and 171 cobs from Test 5. The two groups were treated separately, since Bird regarded cobs from Test 5 as older than those from Test 1, and were designated Huaca Prieta 5 and Huaca Prieta 1, respectively. Cultures responsible for the Huaca Prieta middens began about 3000 B.C. (Bennett, 1948; Bird, 1948), but maize did not make its appearance there until 850 B.C. (Bird, personal communication, 1953). Implications as to archaeological and botanical significance of these finds are further discussed by Anderson (1947b), Carter (1950), and Whitaker and Bird (1949). The well-preserved, tapered and cigar-shaped cobs are remarkably uniform, especially those found in the lower levels, which have small shank diameters, an average row number of 14, and are horny rather than brittle or bony in texture. Thirty-five cobs from Huaca Prieta 1, representing 7 layers, and 44 cobs from Huaca Prieta 5, representing 5 layers, were examined.

ASIA

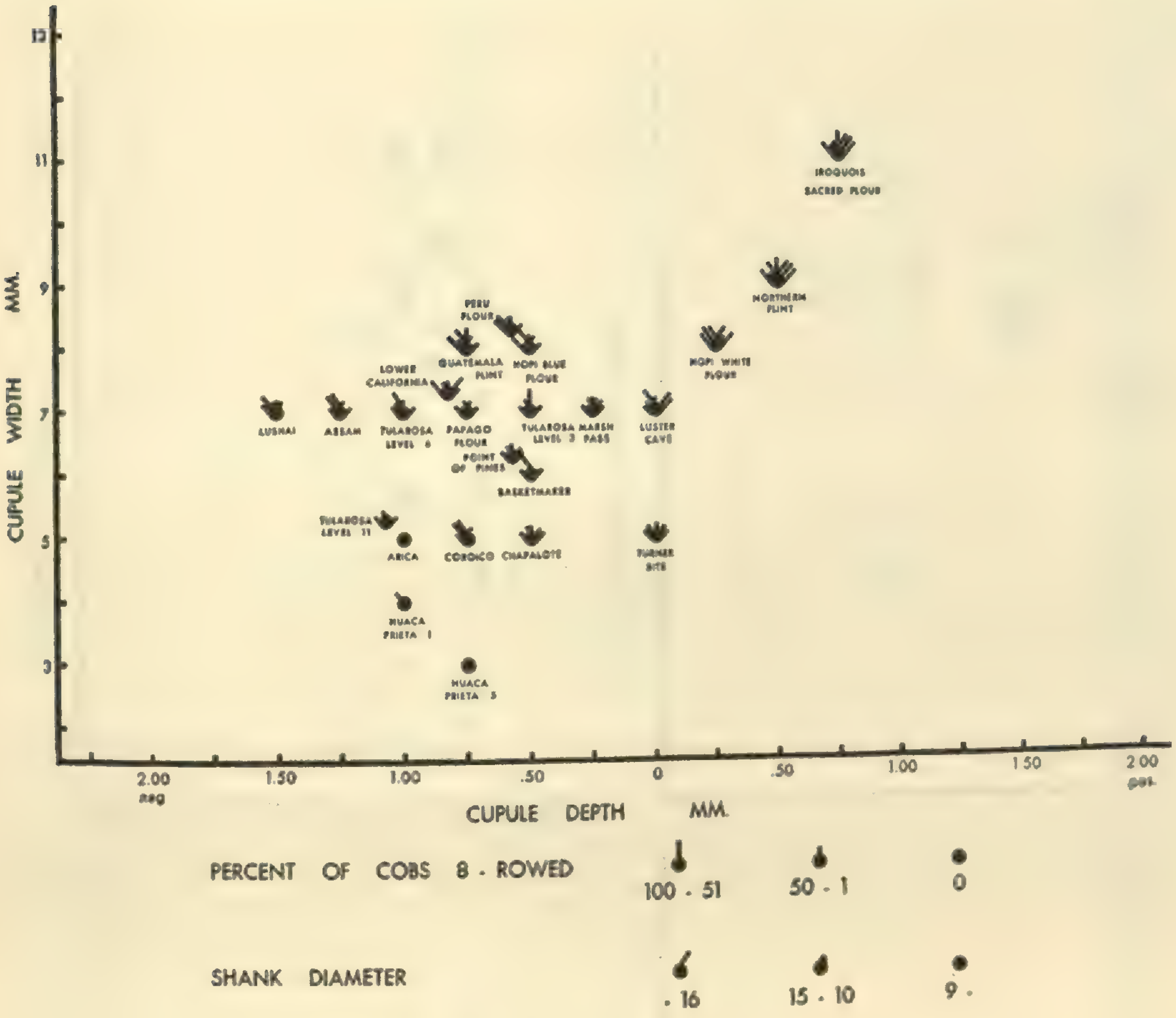
Assam and Lushai.—The samples from Asia were contributed by Stonor, who collected them in the hills of Assam. The history and morphology of varieties in this collection have been described by Stonor and Anderson (1949). The cobs used here were those actually raised in Asia. For this investigation they were separated into two groups: (1) *Assam,* which includes 21 cobs from tribes other than the Lushai; (2) *Lushai,* which includes 8 cobs representative of the maize varieties grown by the Lushai tribe. Cobs of both groups are sufficiently alike to

TABLE I

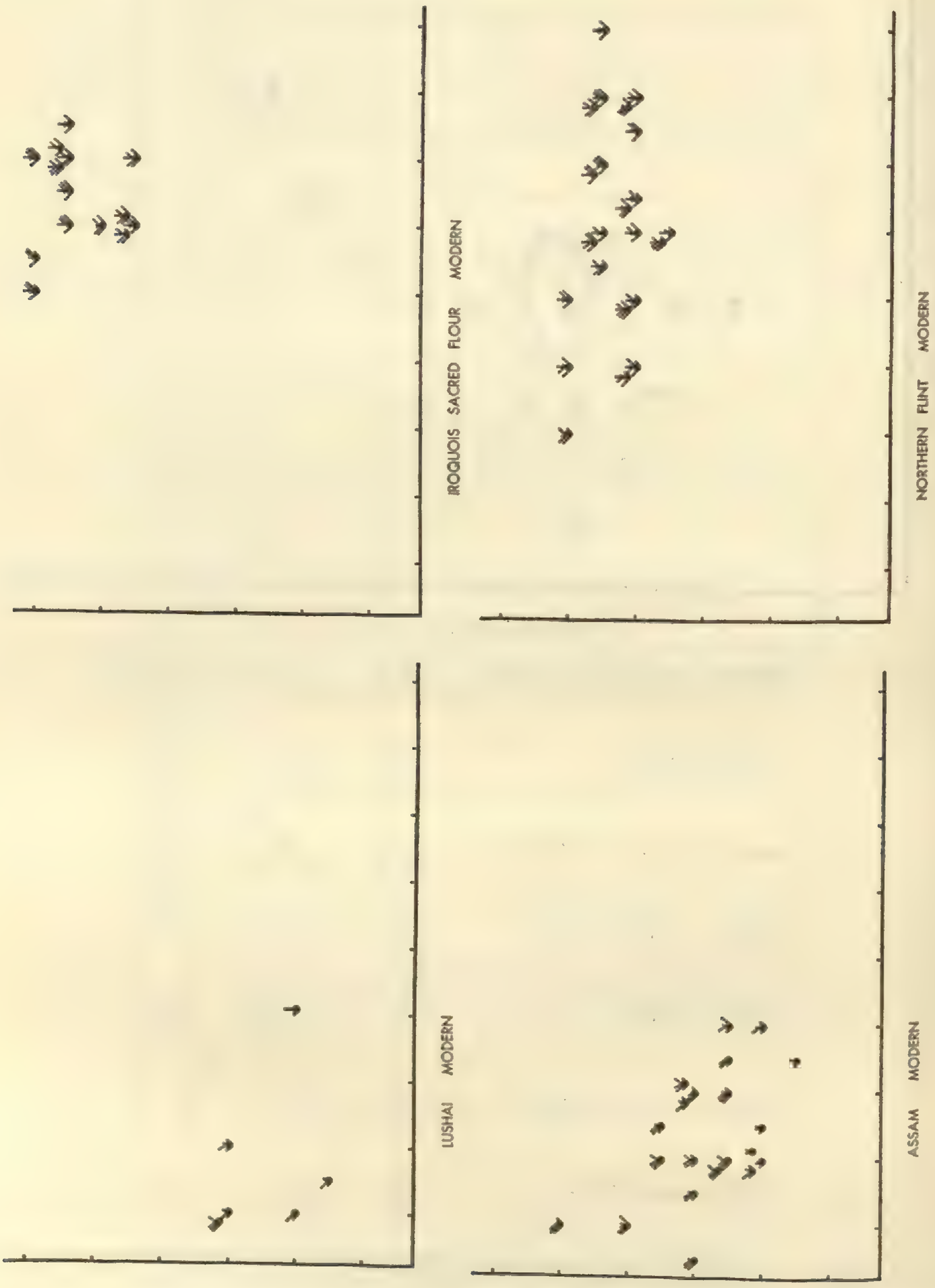
AVERAGE VALUES OF NINE MORPHOLOGICAL CHARACTERS AND TWO INDICES FOR EACH MAIZE COB SAMPLE STUDIED

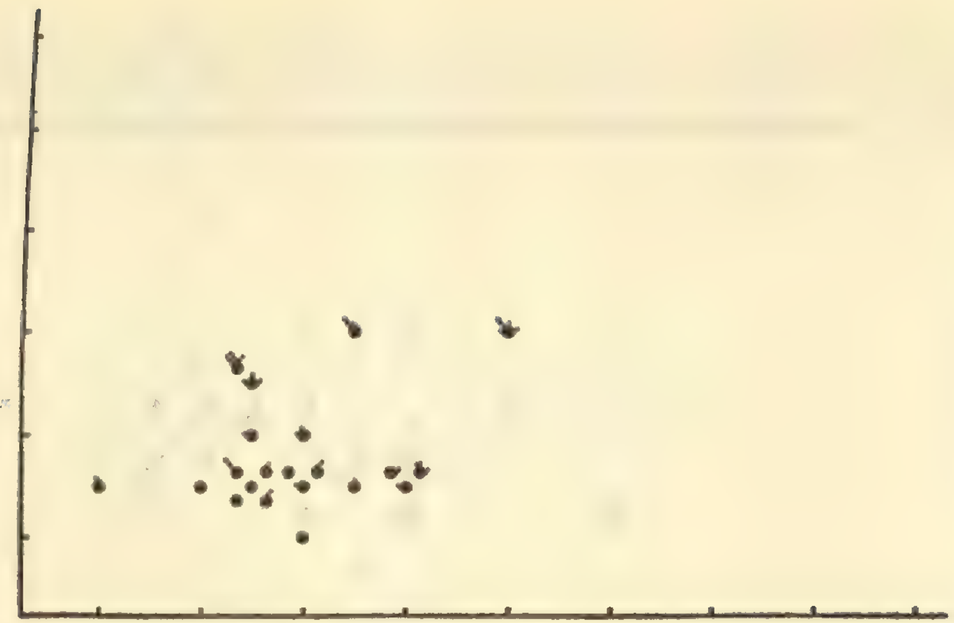
(Measurements in mm. except where otherwise indicated)

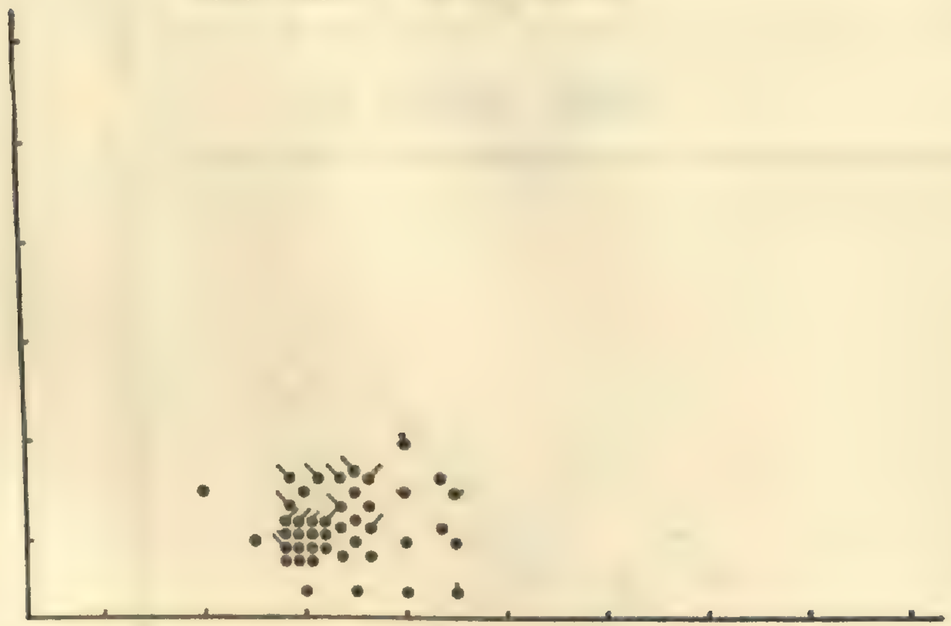
Name of Sample	Cupule		% cobs 8-rowed	Shank diameter	% cobs straight	Height of rachis flaps	Kernel thickness	% cobs tapered	Lower gl. width	Cob/rachis index	Rachis/pith index
	width	depth									
Iroquois Sacred Flour	11.5	+ .75	90	22	43	2.0	3.7	43	8.7	1.7	2.1
Northern Flint	9.5	+ .50	90	16	35	2.0	4.4	32	7.0	1.8	2.1
Hopi White Flour	8.5	+ .25	0	19	35	2.0	4.7	65	6.2	1.7	1.8
Hopi Blue Flour	8.5	— .50	20	12	35	1.6	4.2	0	5.8	1.9	1.8
Papago Flour	7.0	— .75	0	14	0	1.2	4.0	28	5.4	1.8	1.9
Basketmaker	6.0	— .50	0	9	0	1.5	4.3	16	4.4	1.6	2.0
Marsh Pass	7.5	— .25	20	11	16	1.5	4.1	20	5.5	1.5	2.1
Turner Site	5.5	0	11	8	12	1.0	3.0	50	3.7	1.3	1.7
Luster Cave	7.5	0	33	7	33	1.6	4.5	33	5.2	1.8	1.8
Tularosa Cave—L. 3	7.0	— .50	68	9	0	1.5	4.1	4	5.9	1.8	2.4
Tularosa Cave—L. 6	7.5	—1.00	16	7	4	1.3	4.7	48	5.5	1.7	2.3
Tularosa Cave—L. 11	5.5	—1.00	0	8	0	1.0	4.0	4	5.5	1.7	2.3
Point of Pines	6.5	— .50	32	8	20	1.2	3.6	3	5.5	1.7	2.0
Chapalote	5.5	— .50	10	9	0	1.0	4.0	10	5.4	2.1	2.5
Guatemala Flint	8.5	— .75	77	15	0	1.2	4.5	44	6.8	1.9	2.9
Lower California	8.5	— .75	14	8	37	1.3	3.8	27	5.9	1.8	2.1
Peru Flour	8.0	— .50	10	8	8	.9	4.0	92	5.0	1.9	2.2
Coroico	5.5	— .75	0	13	0	.5	6.6	95	5.9	1.9	2.1
Arica	5.0	—1.00	0	6	0	.5	3.2	30	3.5	1.6	2.1
Huaca Prieta 1	4.0	—1.00	0	4	5	.3	3.1	31	2.4	1.6	1.8
Huaca Prieta 5	3.5	— .75	0	6	9	.2	3.0	13	2.7	1.9	1.9
Assam	7.0	—1.25	0	12	0	.9	4.9	75	5.0	1.7	2.3
Lushai	7.0	—1.50	12	10	0	.5	4.0	75	6.0	1.9	2.0

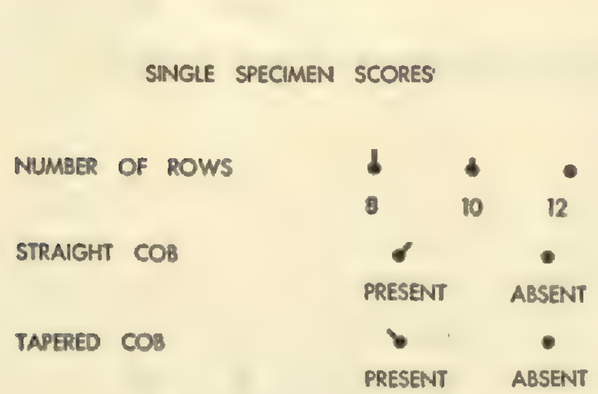


Text-fig. 2. Pictorialized scatter diagram of information contained in Table I, showing relationships between variation in nine different cob characters for various samples of maize. Each dot represents the mean for nine measured characters for all cobs studied in that group; horizontal axis, depth of cupule; vertical axis, width of cupule; seven other characters are diagrammed by rays, as explained on the figure. Further explanation in the text.


IROQUOIS SACRED FLOUR MODERN
NORTHERN FLINT MODERN
LUSHAI MODERN
ASSAM MODERN

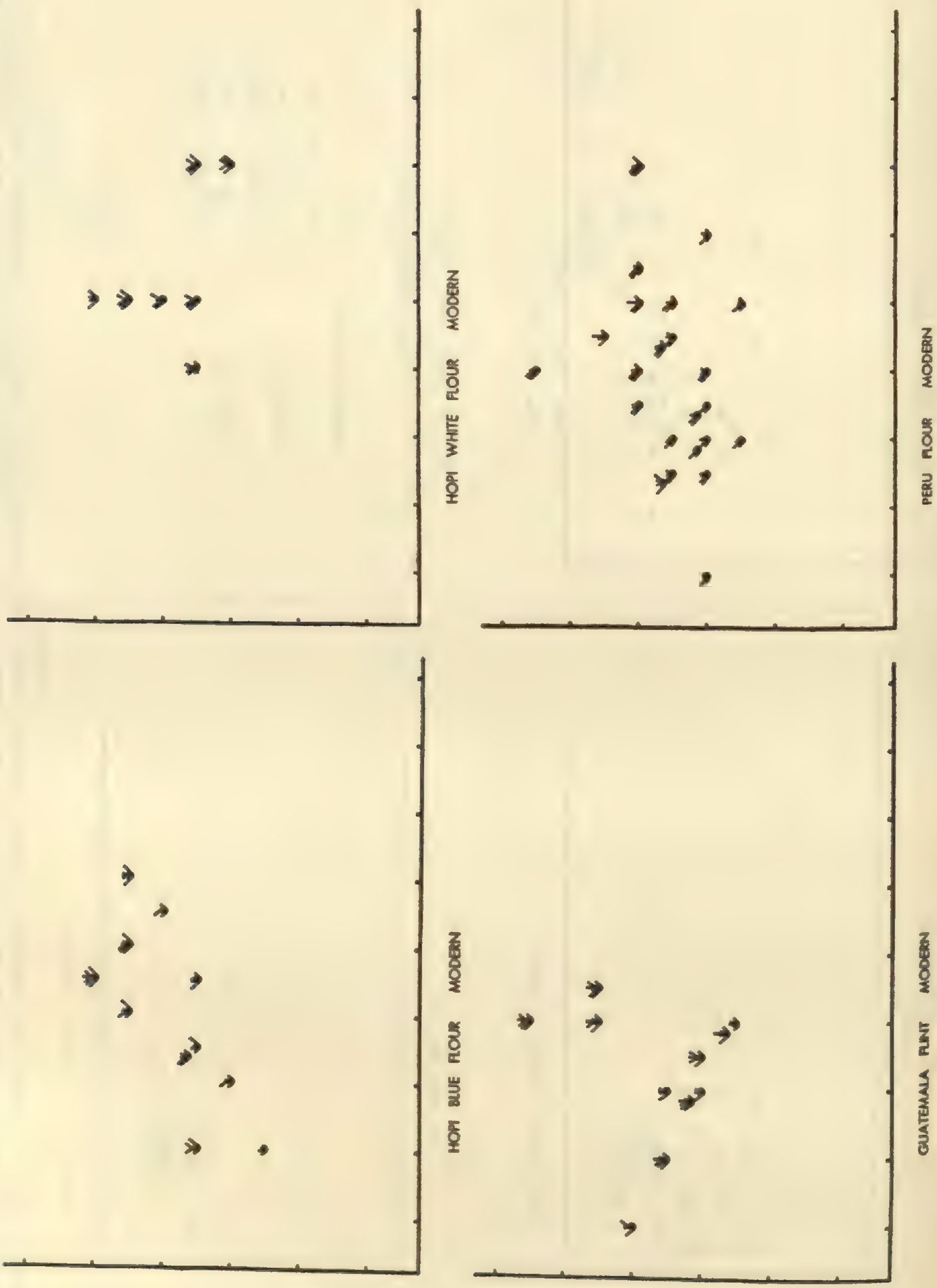


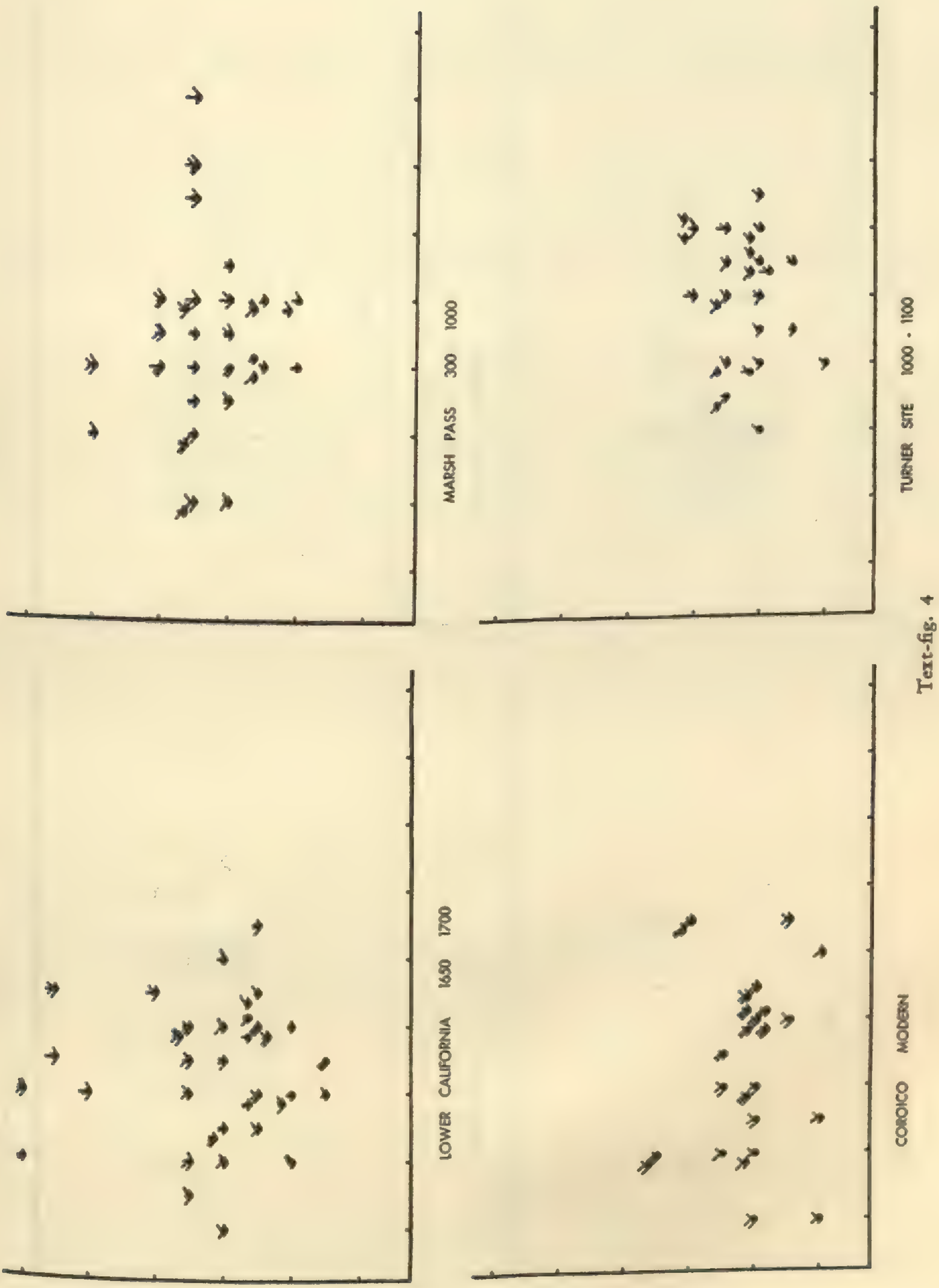




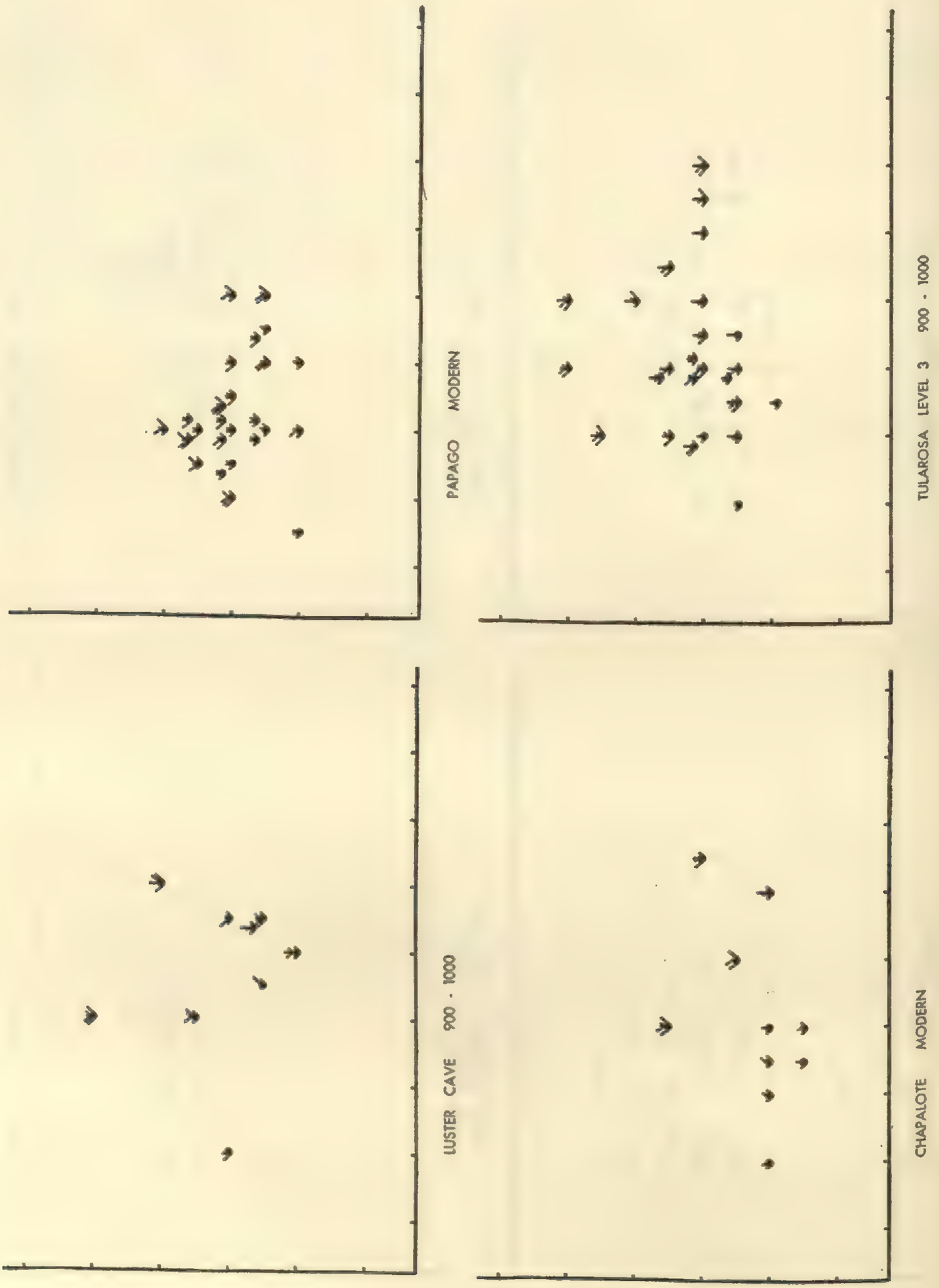
Text-fig. 3

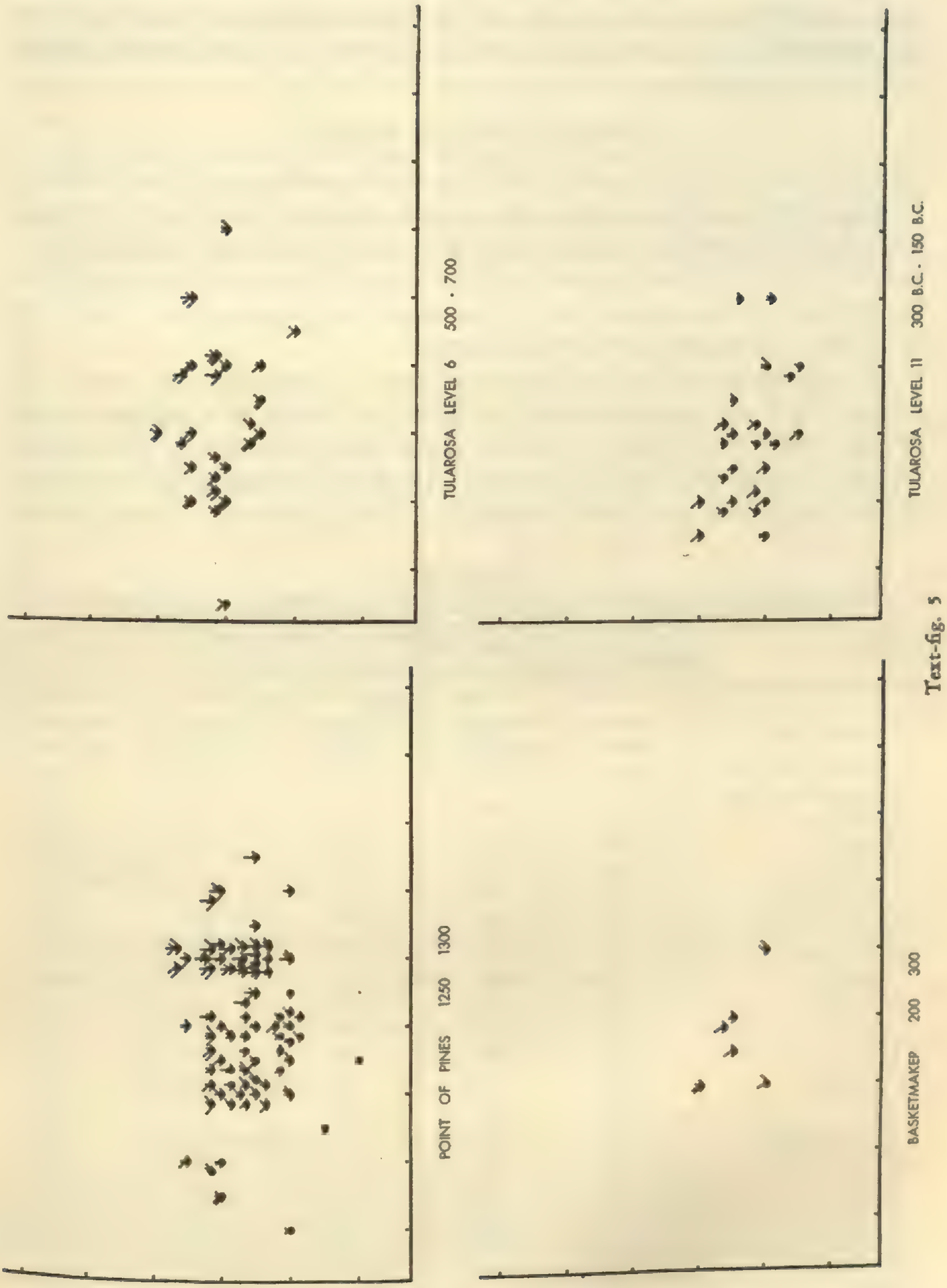
Text-figs. 3, 4, 5. Twenty-three pictorialized scatter diagrams showing the variation and relationships of nine measured characters within each group of maize cobs studied. Each dot represents the actual measurements for one ear. Horizontal and vertical axes and seven additional characters are scored as in text-fig. 2, except row number and cob shape, which were scored as indicated in the lower right-hand corner of text-fig. 3. Dotted ray indicates no measurement could be made.


HOPI WHITE FLOUR MODERN
PERU FLOUR MODERN
HOPI BLUE FLOUR MODERN
GUATEMALA FLINT MODERN


MARSH PASS 300 1000
TURNER SITE 1000 - 1100
LOWER CALIFORNIA 1650 1700
COROICO MODERN

Text-fig. 4


PAPAGO MODERN
TULAROSA LEVEL 3 900 - 1000
LUSTER CAVE 900 - 1000
CHAPALOTE MODERN


TULAROSA LEVEL 6 500 - 700
TULAROSA LEVEL 11 300 B.C. - 150 B.C.
POINT OF PINES 1250 1300
BASKETMAKER 200 300

Text-fig. 5

conform to the same general description. They are tapered, 15–25 cm. in length, with a medium-sized shank and bore 14–16 rows of narrow kernels. That they are markedly lighter in weight than ears of North and Central American maize of comparable size is undoubtedly another expression of their lack of heavily sclerenchymatized tissues.

MEASUREMENTS OF SAMPLES

The number of cobs in each of the above-listed samples varied, but an attempt has been made to examine enough cobs to form consistent pictures of variation in the populations represented. Measurements recorded for each cob include, in addition to those of four external and five internal characters mentioned earlier, diameters of cob, rachis, and pith. From these last measurements, a cob/rachis index and a rachis/pith index were computed.

Since plants are affected by their environment in numerous ways, several representatives of any population must be studied to formulate a complete picture of their range of variation. This idea applies quite as much to archaeological remains as to living plants, for, as Cutler (1952) has pointed out, a single specimen of any archaeological plant remains is of little significance; it may represent

TABLE II

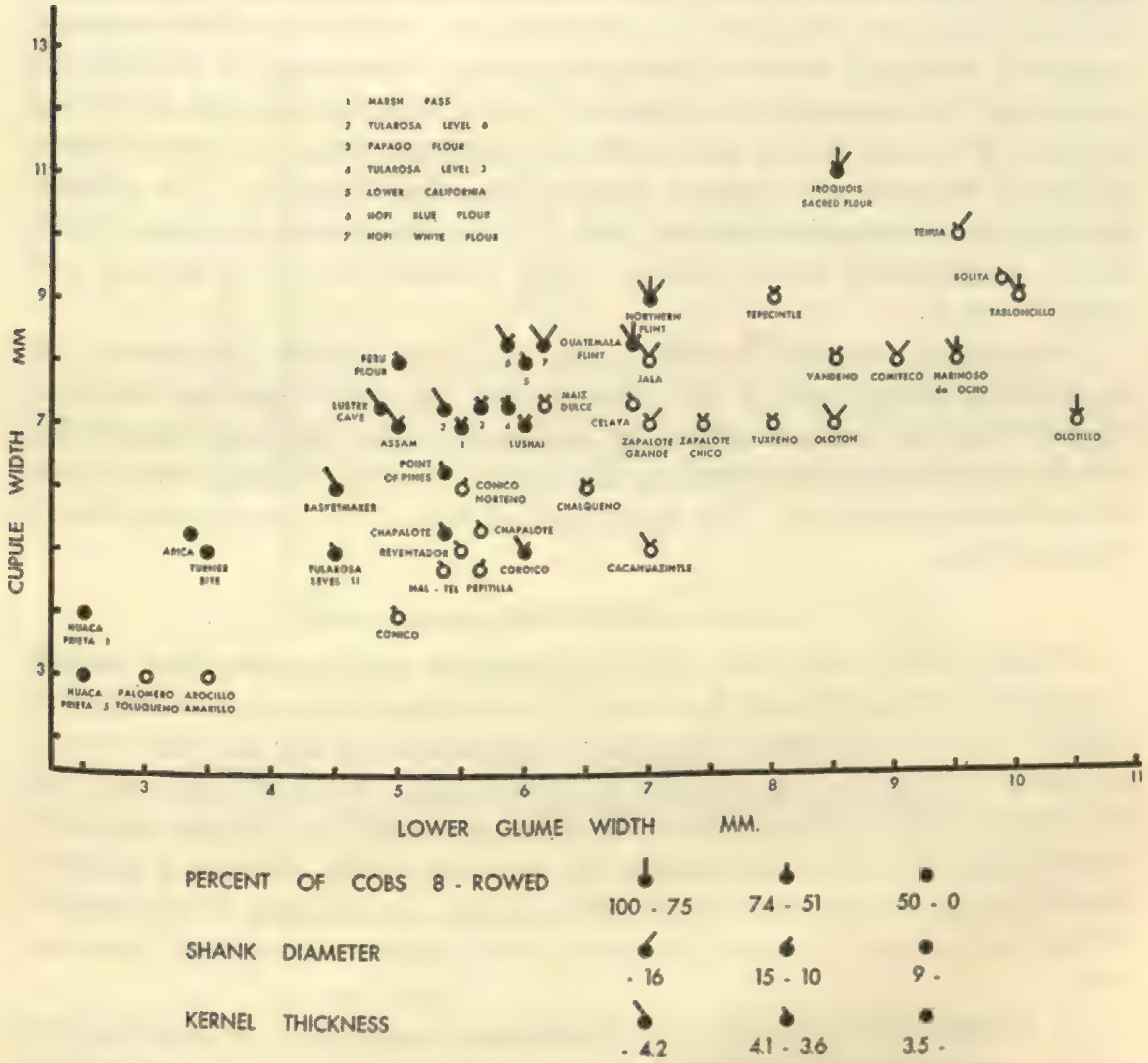
AVERAGE VALUES OF FIVE MORPHOLOGICAL CHARACTERS FOR TWENTY-FIVE EXISTING RACES OF MAIZE IN MEXICO (DATA FROM WELLHAUSEN *ET AL*, 1951, 1952).

(Measurements in mm. except where otherwise indicated.)

Name of race	Cupule width	Width of lower glume	% cobs 8-rowed	Shank diameter	Kernel thickness
Palomero Toluqueño	3.0	3.0	0	8	2.8
Arocillo Amarillo	3.5	3.5	0	8	2.5
Chapalote	5.5	5.5	20	9	4.1
Nal-Tel	5.0	5.5	20	7	3.9
Cacahuazintle	5.0	7.0	0	10	5.2
Harinoso de Ocho	8.0	9.5	100	14	4.4
Olotón	7.0	8.5	20	17	6.0
Maíz Dulce	7.0	6.0	0	11	4.0
Cónico	4.0	5.0	0	8	3.6
Reventador	5.0	5.5	20	8	3.6
Tabloncillo	9.0	10.0	90	11	4.3
Tehua	10.5	9.5	0	21	3.9
Tepecintle	9.0	8.0	0	10	3.7
Comiteco	8.0	9.0	0	22	4.5
Jala	8.0	7.0	0	34	4.6
Zapalote Chico	7.5	7.5	20	13	3.6
Zapalote Grande	7.5	7.0	0	18	3.8
Pepitilla	5.0	5.5	0	12	3.5
Olotillo	7.5	10.5	90	10	3.9
Tuxpeño	7.5	8.0	20	13	3.7
Vandeño	8.5	8.5	0	13	3.6
Chalqueño	6.0	6.5	0	10	3.9
Celaya	7.5	7.0	20	9	3.9
Cónico Norteño	6.0	5.5	0	11	3.5
Bolita	9.0	10.0	50	9	4.1

an accidental deposition, or it may have been buried in an old layer or brought to a recent one by rodents, pot hunters, or a recent occupant of the site. To minimize these effects, arithmetic averages of the measurements of each character have been computed for each sample. Alava (1952) pointed out that such a technique provides the only safe basis for studying variation between different varieties of plants.

Table I lists the average values for each of the characters of each sample studied. Ear shape contributed two columns, one for straight ears and one for tapered ears, thus giving a total of nine characters in which to compare variation. A pictorialized scatter diagram of these same results is presented in text-fig. 2.



Text-fig. 6. Pictorialized scatter diagram of material from Tables I and II showing relationships between variation in five different cob characters among the twenty-five races of maize in Mexico (data of Wellhausen *et al*, 1951, 1952) and the twenty-three samples of the present study. Each dot represents the average measurements of five characters for all maize cobs studied in that group; horizontal axis, width of lower glume; vertical axis, width of cupule; three other characters are diagrammed by rays as explained on the figure. Further explanation in the text.

Text-figs. 3, 4, and 5 show the variation and relationships of these same nine cob characters within each sample of cobs. The method of construction, as well as the general usefulness and reliability of these diagrams, is further discussed below.

An attempt was made to compare the results of this investigation with those obtained by Wellhausen *et al* (1951, 1952) for races of maize in Mexico. Several of the major characters employed in the present study were not employed by Wellhausen and his co-workers. However, their paper contained excellent diagrams of cross-sections of ears of each race drawn to scale; it was possible to make certain measurements directly from these diagrams. Lower glume width in mm. was measured at the widest point indicated on the third concentric circle of each ear diagram. Cupule width in mm. was measured as a straight-line distance across the bases of any two consecutive kernels from the points where their boundaries intercepted the rachis diameter (innermost circle). Percentage of 8-rowed ears was obtained by comparing the number of rows in each drawing with the average values listed for each race in their Table 15. Average values for shank diameter and kernel thickness were obtained directly from their Table 15. The information obtained is summarized here in Table II; it is also presented as part of text-fig. 6, a pictorialized scatter diagram which compares related data from both Tables I and II.

Male spikelet variation has been studied by Alava (1952) for seven of the twenty-three samples used in this investigation. A crude index has been constructed after the manner outlined by Anderson (1936) for both Alava's data and the appropriate data set forth in text-fig. 2. Text-fig. 7 shows the relationships of these index values. The significance of each of the above comparisons is discussed below.

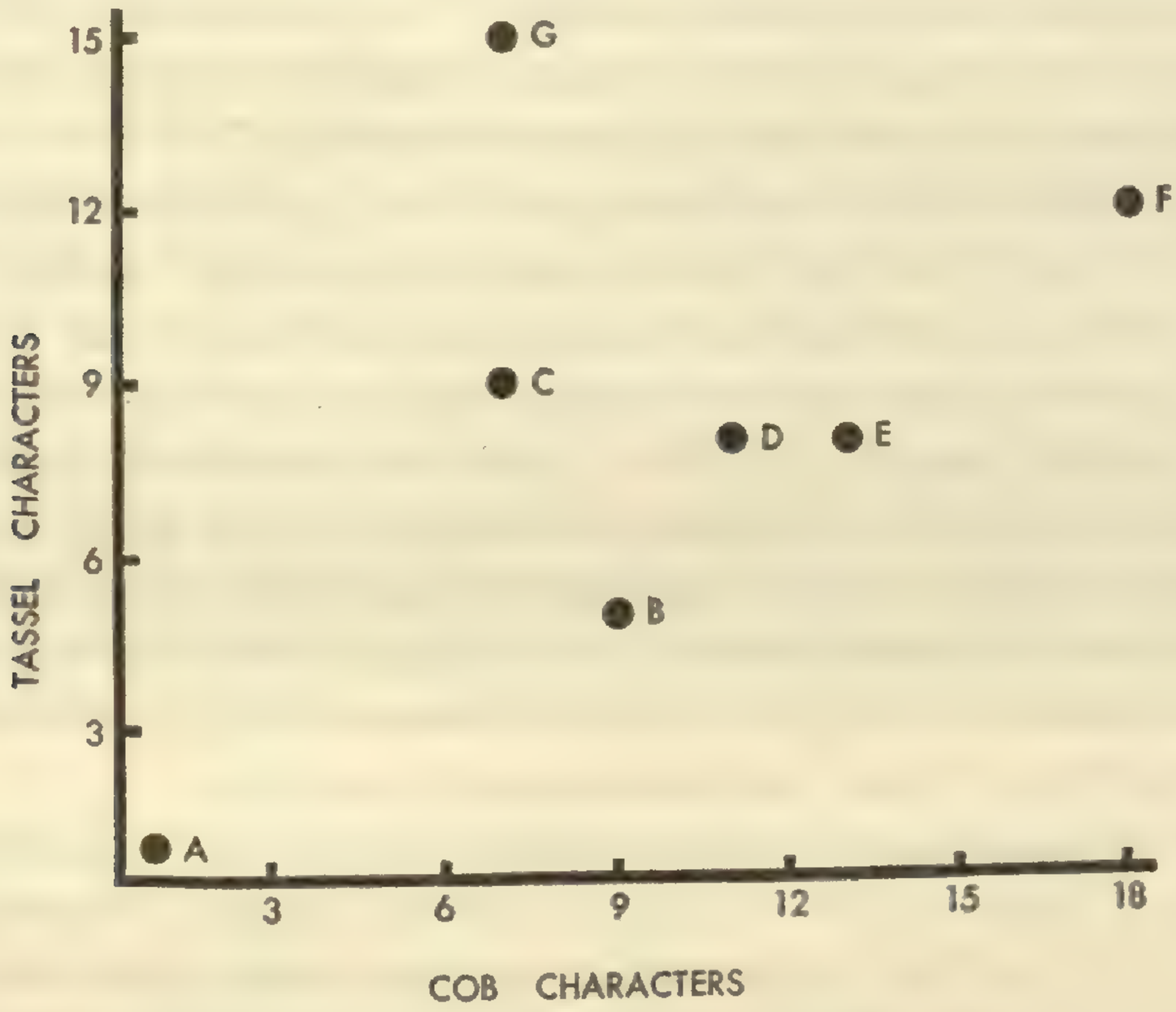
DISCUSSION

Whiting (1944) and Cutler (1951) pointed out that botanists alone probably cannot solve the problem of the origin of maize, because maize is so intimately linked with human cultures. This point is emphasized by the fact that maize is completely dependent upon man for its preservation. Whatever may have been the original factors leading up to this novel situation, the fact remains that maize and man have been associated together for quite some time, and that a consideration of changes in maize types in any given locality over a period of years involves a study of changes in human cultures for that same locality during those same years.

In a study which involves the disciplines of ethnology, archaeology, and botany, caution must be exercised lest theories proposed in one science be regarded as proven facts by workers in another. Since the present investigation has been conducted from the standpoint of botany, such conclusions as can be drawn should depend in so far as possible upon botanical evidence for their support. To this end, botanical information is discussed first, and an attempt is then made to relate this discussion to known facts of ethnology and archaeology.

Botanical Aspects of Maize Cob Analysis

Variation among races of maize is nowhere better illustrated nor more difficult to describe than that found among female inflorescences, or cobs. Within any race, many cobs possess characters the measurements of which lie well within the range of variation of the same measurements from several other races. This exasperating fact is true for all the characters used in this study. Using any one cob character at a time, it is nearly impossible to distinguish races of maize; it is for this reason that the empirical classification of maize by kernel types proposed by Sturtevant (1899) is not of much value to modern maize breeders. Mangelsdorf and Reeves (1939) used evidence from several sources to characterize maize from different parts of the New World. Anderson (1946, 1947a), Anderson and



INDEX VALUES

MAIZE	RACE	COB CHARACTERS	TASSEL CHARACTERS
A	ARICA	1	1
B	ASSAM	9	5
C	CHAPALOTE	7	9
D	PERU FLOUR	11	8
E	GUATEMALA FLINT	13	8
F	NORTHERN FLINT	18	12
G	PAPAGO	7	15

Text-fig. 7. Scatter diagram of index values of seven races of maize in which both the tassel (male inflorescence) and the cob (female inflorescence) have been investigated. Horizontal axis, index values derived from cob study; vertical axis, index values derived from tassel study. Further explanation in the text.

Cutler (1942), Mangelsdorf and Smith (1949) and Wellhausen *et al* (1951, 1952) have used an increasing number of subtler characters in distinguishing both modern and prehistoric races of maize.

Pictorialized scatter diagrams (Anderson, 1949b) are a means by which several such variable characters can be considered at once, thereby emphasizing consistent and typical differences as well as similarities among the particular entities involved. Methods by which a pictorialized scatter diagram is developed are explained by Anderson (1949b, 1952) and Anderson and Gage (1952). Anderson (in press) has discussed the biological and mathematical criteria upon which pictorialized scatter diagrams are based. The value of such diagrams has been emphasized by Stebbins (1952), who considered the method "by far the best yet devised for making the observer aware of a pattern of variation in respect to three or more characters which are varying simultaneously." He also stated (1952) that the method "has the advantage of being repeatable and of focusing the attention of the observer upon certain essential features of variation."

The data listed in Table I have been plotted as a pictorialized scatter diagram (text-fig. 2) to show how the several cob characters are varying and to what extent their variation is correlated. Measurements of depth and width of cupule were chosen as abscissa and ordinate respectively because they varied consistently within each sample (text-figs. 3, 4, 5), could be ascertained from fragmentary cobs, and were susceptible to accurate measurement. The other seven characters were then indicated by rays from each dot of the scatter diagram. Extremes of each character tending to be associated with higher values of cupule width and depth were represented by long rays, while extremes tending to be associated with lower ordinate-abscissa values were represented by no rays.

Several facts concerning the maize samples studied were immediately apparent. At one extreme (upper right-hand corner of the diagram) were predominantly straight 8-rowed cobs with wide, shallow cupules, large rachis-flaps, wide lower glumes, heavy shanks, and thick or moderately thick kernels. This complex of characters was found in Northern Flint and Iroquois Sacred Flour; occurrence of endosperm as flinty or floury is dependent upon a single gene and is therefore of no significance here. These results agreed with those found by Brown and Anderson (1947) for typical Northern Flint varieties; the same complex was identified by Carter and Anderson (1945) as the Eastern complex. At another extreme (lower left-hand corner of the diagram) were cigar-shaped cobs with high row numbers, narrow deep cupules, small rachis-flaps, narrow lower glumes, small shank diameters, and thin kernels. These characters were associated in prehistoric maize recovered at Huaca Prieta, Peru, and Arica, Chile. It is significant that the majority of cobs were essentially complete but only about 5 cm. long. As a whole, these samples were remarkably homogeneous (text-fig. 3). Existence of a third extreme (middle left area of the diagram) is indicatd by tapered cobs with high row numbers, extremely deep cupules, little rachis-flap development, wide lower glumes, medium shank diameters, and thick or moderately thick kernels. The two

maize samples from Asia were responsible. Cobs studied were those grown by Stonor in Asia; varieties involved were described by Stonor and Anderson (1949).

The most striking features of the Asian corn cobs were their extremely deep cupules and their particular form of sclerenchymatization. The rachis tissue and lower glumes of all Asian cobs studied were quite hard, but their hardness was not identical with that of "bony" rachis tissue described by Mangelsdorf and Smith (1949) in connection with teosinte introgression. Whatever its cause, the end product was an extremely stiff, light-weight bulky cob. Studies by Lenz (1948) did not indicate that cell wall thickness had much to do with degree of sclerenchymatization among various races of maize. A deep cupule could possibly be interpreted as a condition which showed little if any "Tripsacoid influence" (Cutler, 1946). An inference cannot be drawn that all Asian maize varieties are alike in this respect, but for both Assam and Lushai samples, this conclusion seems justified.

The nine characters employed in constructing text-fig. 2 showed a strong tendency for association at both extremes. A strong overall association between all sample averages as well as within each sample is clearly shown by comparing the average of any sample in text-fig. 2 with its appropriate population diagram in text-figs. 3, 4, or 5. Individual cobs in the upper right-hand area of each population diagram consistently showed more and longer rays than did those from other parts of the same diagram. This similarity of separation patterns in the several diagrams emphasizes the fact that those limits employed in separating sample averages, while originally chosen in a subjective taxonomic fashion (Stebbins, 1952), were also working within each sample in such a way that morphological trends associated with a particular race of maize were associated with each other.

The diagram as constituted contains samples of rather diverse races of maize; closeness of position on the diagram and similarity of glyphs indicate similar morphology but do not necessarily imply close relationship. Weatherwax (1936) stated that no sound basis exists for any attempt to trace maize origin by arranging varieties from different localities in an evolutionary sequence. Introduction of the dimension of time in the form of archaeological material, however, allows the investigator to arrange maize varieties of both present and past according to cultural succession; the result may or may not be an evolutionary sequence, but such an arrangement is the strongest means available for documenting maize history and has therefore been employed in this investigation whenever possible.

Results obtained in this investigation are compared below with those obtained in three other independently conducted investigations. A high degree of correlation is found in each instance, a fact which indicates a basic soundness in methods employed for cob analysis in this investigation.

Brown *et al* (1952) have discussed relationships among three varieties of Hopi maize, two of which, Hopi White Flour and Hopi Blue Flour, were included in the present study. These workers found that the two varieties had certain re-

semblances to Basketmaker and Eastern maize as well as to each other. Unfortunately, it was not possible to obtain a large enough sample of Kokoma, the variety they reported as resembling Basketmaker most closely, to warrant its inclusion here. Text-fig. 2 indicated that Hopi Blue Flour was basically similar to Basketmaker, differing in cupule width, wide lower glumes, heavy shanks, and presence of 8-rowed cobs. It should be noted that there has been no change in cupule depth and predominance of cigar-shaped ears in development of Hopi Blue Flour from Basketmaker maize.

Hopi White Flour was found by Brown *et al* (1952) to contain an admixture of both Eastern and Mexican germ plasm. The Mexican complex (Carter and Anderson, 1945), known to be present on the Mesa Central of Mexico, is characterized by strongly tapered cobs with high row numbers, thick kernels, and small shanks. This conclusion was borne out by text-fig. 2, which showed Hopi White to have all the characters associated with the Eastern complex with the exception of row number and cob shape; tapered cobs of high row number may be attributed to Mexican influence. Cobs of these two Hopi Flour maizes differed from each other in cupule depth (text-fig. 2 indicates this to be the strongest character contributed by the Eastern complex), cob shape, shank diameter, rachis-flap height, and row number.

In the correlation between results obtained in the present investigation and those of Wellhausen *et al* (1951, 1952) which are listed in Table II, the number of characters used was less than the number employed to separate the samples listed in Table I; yet, a pictorialized scatter diagram (text-fig. 6), using five measurements, presented essentially the same variation pattern as did text-fig. 2, in which nine measurements were employed. It should be noted that the basic pattern of maize cob variation was not altered by using measurements of a different character for the abscissa of text-fig. 6 than that employed in text-fig. 2. If a sample on text-fig. 6 has any real affinity to races with which it may be allied on other grounds, the fact should be shown by its position on the diagram. Text-fig. 6 should also lend further confirmation to the genealogies postulated by Wellhausen *et al* for several hybrid races of maize. That these confirmations are indeed possible was shown quickly and easily. The four races classified by these workers as Ancient Indigenous Races (Palomero Toluqueño, Arocillo Amarillo, Chapalote, Nal-Tel) were closely grouped; moreover they were all placed in the lower left-hand corner of the diagram and all had few to no rays. Thus their characters of small cupules, narrow lower glumes, high row numbers, thin kernels, and small shanks, all believed to indicate primitiveness in relation to other races of maize here considered, were strikingly indicated by text-fig. 6.

Three of the four races classified as Pre-Columbian Exotics (Cacahuazintle, Harinoso de Ocho, Olotón, Maíz Dulce) formed a consistent graded series along the lower edge of the upper region of text-fig. 6. They were placed in a separate class because of their antiquity and resemblance to South American maize. While

the class was somewhat artificial, the positions of three of its four constituents on the diagram in a nearly perfect ascending order indicated a basic similarity in variation pattern.

From these races a group of thirteen Prehistoric Mestizos and a group of four Modern Incipient races were thought to have arisen. For many of these, Wellhausen *et al* compiled a chart showing the two putative parents of the particular race under discussion. Out of a total of eleven genealogical relationships involving other races plotted on text-fig. 6, seven were found to be borne out by diagram position, being for the most part midway in both position and number of rays. These genealogical relationships as postulated by Wellhausen *et al* are listed below. Group 1 is comprised of those races whose positions on text-fig. 6 offered further proof of relationship to their putative parents. Group 2 is comprised of those races whose positions on text-fig. 6 did not approximate positions between their putative parent races.

GROUP 1

Cónico	Palomero Toluqueño	×	Cacahuazintle
Zapalote Chico	Nal-Tel	×	Tepecintle
Chalqueño	Cónico	×	Tuxpeño
Cónico Norteño	Celaya	×	Cónico
Bolita	Zapalote Chico	×	Tabloncillo
Tuxpeño	Tepecintle	×	Olotillo
Comiteco	Tehua	×	Olotón

GROUP 2

Zapalote Grande	Tehua	×	Zapalote Chico
Vandeno	Tuxpeño	×	Zapalote Grande
Celaya	Tabloncillo	×	Tuxpeño
Jala	Tabloncillo	×	Comiteco

The fact that a majority of such genealogies can be substantiated by arranging data obtained from the cobs alone is added proof that races may not only be recognized by cob characters, but that their histories can also be ascertained in the same manner with a high degree of accuracy. It should also be borne in mind that data for the Mexican samples represented averages determined from 3–5 cobs of each race; the accuracy might well have been increased had more cobs been used in determining average values. Text-fig. 6 further showed that variation in Mexican maize followed the same general pattern of character association as did variation among the samples employed in this investigation, and that prehistoric North and South American samples were close to the primitive Mexican races.

Spikelet variation in *Zea Mays* was studied by Alava (1952), using methods which, while applicable to male inflorescences, were of no use in the investigation of maize cobs. Thus if any correlation between results of two independently conducted investigations should exist, it would not only be further substantiation for validity of methods employed and results obtained, but also would indicate that cob and tassel analyses yield comparable results. Similar material from seven different races was examined in each investigation. A numerical index (Anderson,

1936; Stebbins, 1952) for both cob and tassel characters was computed for each race. While admittedly a crude indicator of morphological characters, numerical indices are valuable for summarizing diverse data in a manner which permits direct comparisons to be made. Text-fig. 7 shows the extent of this correlation. Arica had the smallest value in both indices, and there was a general progression toward the upper right-hand corner of the graph occupied by Northern Flint. Papago appeared somewhat aberrant as far as tassel index was concerned, but came closest to Chapalote, a related race, in both values. Peru Flour and Guatemala Flint were close, a further expression of their presumed relationship to one another. Guatemala Flint was closer to Northern Flint for cob-index value. Although a considerable number of units away, Asian material was closest to Arica in both cob and tassel values. Thus with the possible exception of Papago, in which variation is unique but consistent with its past history, the samples showed high correlation between tassel and cob morphology in distinguishing races of maize.

Maize Cob Analysis in Relation to Ethnology and Archaeology

Knowledge of ancient peoples is in large part built upon a detailed study of their refuse heaps; rubbish being what it is, a place is assured for the botanist in archaeological analysis. Analysis of maize remains is especially helpful, since few other plants have become so closely associated with man to the extent that they are reliable indicators of his early history in many parts of the New World.

SOUTH AMERICA AND ASIA

Lowie (1940) pointed out that it was a common mistake to identify all early agriculture with maize. Sauer (1952) contended that seed-crop agriculture was developed after a root-crop agriculture which involved vegetative propagation only. Excavations in northern Chile (Bird, 1943), and more especially in Peru (Bennett, 1948; Bird, 1948), showed that there were indeed agricultural communities without maize. Layers of middens at Huaca Prieta, Peru, beginning about 4000 years ago, contained squash, beans (4 types), chili peppers, *Canna,* cotton, and bottle gourds (*Lagenaria siceraria,* Whitaker and Bird, 1949). Maize did not appear until 850 B.C. Whitaker (1948) pointed out that it is extremely difficult to account for the bi-hemispheric distribution of *Lagenaria,* as it is presumed to be of Asiatic origin. Partly on such distributional patterns, Carter (1950) postulated pre-Columbian contacts between the Old and New Worlds, a theory also put forward by Stonor and Anderson (1949) and Sauer (1952). That it was quite possible to sail in either direction across the broad expanse of the Pacific has been amply documented by Buck (1938).

Another odd fact about prehistoric plants of west-coast South America is that they are presumed to be native to Central America. Either these plants reached the coast as articles of trade among established peoples, or they were taken there by the first settlers of the area, who either came from or passed through the Cen-

tral American region. It does not seem possible that maize would have been overlooked by these peoples as a crop plant had they passed through an area in which it was growing or being grown. Yet evidence on the possible antiquity of maize in central Mexico was recently reported by Barghoorn (1952). Maize pollen has apparently been recovered from sedimentary deposits under Mexico City which may antedate human occupation. Recently, however, the date of human occupation has been pushed back to 9000 years in the same area (Richards, 1953).

A type of maize hitherto not mentioned in this investigation is that which is generally referred to as popcorn. True pops are generally of quite primitive morphology (Mangelsdorf and Smith, 1949). Prehistoric Arica and Huaca Prieta maize remains may quite possibly be those of popcorns; Wissler (1945) showed that this is true for some whole maize ears excavated at Arica. In ear shape and size and in tassel characters (Alava, 1952), these prehistoric remains were comparable to a modern pop variety collected by Parodi in Argentina. They may also be related rather closely to Asian types, since they had deep cupules, high row numbers, and some tapered cobs. Tassel analysis (Alava, 1952) also showed an Asian similarity. The above evidence is suggestive, but it also indicates the necessity for more data before the history of maize in both South America and Asia can be considered to be completely known.

THE AMERICAN SOUTHWEST

Maize in the American Southwest has had a long and complicated history. Man was present in the area 10,000 years ago (Wormington, 1949; Johnson, 1951) but there was little evidence that the area was under continuous occupation from that time until the advent of agriculture. Randolph (1952) stated that an apparently humid and subtropical climate existed there 5,000–10,000 years ago, and that the area itself could be the original home of maize. Carter (1945) likewise postulated the Southwest as a center of agricultural dispersal. All known archaeological remains which contain maize are younger than 5,000 years, so the problem at present is to evaluate the evidence at hand. It should be kept in mind that whatever statements are made below are subject to revision in the light of further discoveries.

Carter and Anderson (1945) noted three major cultural provinces in the Southwest: Hohokam, Mogollon, and Anasazi (Puebloan). At the time of their survey, little was known of the Mogollon civilization, but recent excavations at Tularosa and Cordova Caves (Martin *et al*, 1952) have produced evidence establishing this cultural province as one of equal importance with Hohokam and Anasazi. Archaeological maize is now known for each of the three cultural provinces. Hohokam maize was found in Ventana Cave, Arizona (Haury, 1950). It is similar to but not identical with modern Pima-Papago varieties (Carter and Anderson, 1945). Chapalote, an ancient Mexican race, is today found in northwestern Mexico, an area which was also part of the Hohokam cultural province (Amsden, 1949). Relationships between Papago and Chapalote have been dis-

cussed above. Since the Hohokam area was relatively isolated from influences of neighboring cultural patterns, the maize found there today is much the same as it was in ancient times. It is reasonable to assume that prehistoric maize in this cultural province was similar but not identical to that of Basketmaker and Mogollon cultures, and that modern Papago and Chapalote were derived from it. It was shown (text-fig. 2) that maize remains recovered from Tularosa Cave Level 11 were quite similar to both Chapalote and Basketmaker. Similarity between Chapalote and Basketmaker II maize from Cottonwood Cave (Hurst, 1948; Hurst and Anderson, 1949) was pointed out by Wellhausen *et al* (1951, 1952). Amsden (1949) noted the similarity of modern Papago to Basketmaker, as did Carter and Anderson (1945). The present investigation showed that Basketmaker resembled Chapalote much closer than it did Papago, but the important point is that all three cultural areas, Hohokam, Anasazi, and Mogollon, had at an early date maize which was variable but essentially similar. Maize of the Hohokam area remained relatively unchanged; that of the other two areas was strongly influenced by maize from more remote places. Text-fig. 5 illustrates the variable nature of early southwestern samples. In contrast to maize of the Southwest, remains from Arica, Chile, and Huaca Prieta, Peru, are very homogeneous; furthermore, maize of these two areas (American Southwest and South American West Coast) were contemporary. Explanation of the variability in the one location and homogeneity in the other at the same time is but one of the many problems of maize history.

Basketmaker maize was widespread, having been reported from several sites in the Anasazi area. Some of the better known sites are Cottonwood Cave, western Colorado (Hurst, 1948; Hurst and Anderson, 1949), Mummy Cave, Cañon del Muerto, Arizona (Anderson and Blanchard, 1942), and Painted Cave, northeastern Arizona (Haury, 1945). Basketmaker-like maize was reported outside the Anasazi area by Brown and Anderson (1947) in prehistoric remains of rock shelters and caves from the Ozarks to southern Ohio.

Two combinations of maize characters, one peculiar to the Mexican Mesa Central and the other to the eastern United States, were superimposed in varying amounts on southwestern maize. The spread of each influence may be traced by analysis of successive samples; in such work, the importance of dated maize remains can hardly be over-emphasized. Mexican influence is characterized by strongly tapered cobs with high row numbers (Carter and Anderson, 1945), thick kernels, and small shanks. This type entered the Southwest from the Northeast rather than from Mexico directly; its greatest influence has been found in remains of the Fremont Basketmakers of Yampa Canyon, Utah, dated at 400–800 A.D. (Burgh and Scoggin, 1948).

At Luster Cave, in extreme eastern Utah, maize was subjected to strong Eastern influence prior to 1000 A.D. Text-fig. 2 showed this sample to be closely related to Hopi White Flour among ethnological races examined in this study. Hopi White Flour differed, however, in being more extreme for certain Mexican (tapered

ears, high row numbers) and Eastern characters (large shanks, wide lower glumes). Maize from the Davis Site (Newell and Krieger, 1949) was analyzed by Jones (1949) and found to be entirely Eastern. These maize remains were dated at about 700 A.D. by Jones and at about 400 A.D. by Johnson (1951).

The question of origin of Eastern influence has long been a puzzling one. Anderson (1947a) and Brown and Anderson (1947) presented evidence that Eastern maize is related to Guatemalan maize. Jones (1949) reported that he and Krieger independently reached the conclusion that both maize and pottery types recovered at the Davis Site bore a resemblance to those of Guatemala. Carter (1946) suggested that maize could have been carried up the east coast of Mexico or across the Gulf to southern United States. Regardless of the method employed, this movement must have taken place in time for the influence to have been carried to the Southwest by 1200 A.D., a date which Carter and Anderson (1945) recognized as closely approximating its first appearance in that region. Judson (1951) called attention to the fact that a great drought occurred in the Southwest in 1276–1299 A.D., and that many Indian tribal migrations took place around that time. The direction of movement of maize into the Southwest was from east to west; Carter and Anderson (1945) noted that among the present-day Puebloan tribes, those of eastern pueblos have more eastern-like maize than do those of western pueblos. It is generally accepted that there is influence of Plains cultures in the southwestern area. This influence also is stronger in eastern pueblos than in western ones, and is another indication of how well maize history is correlated with the history of the peoples who grew it.

THE AMERICAN SOUTHEAST AND EAST

Wherever the Eastern complex came from, it was probably carried up the river valleys of the Mississippi and its tributaries by Indian tribal migrations. A date of 900 A.D. was assigned to the earliest known Burial Mound I culture by Ford and Willey (1941), who also identified the beginnings of horticulture in eastern United States at this time. Burial Mound I peoples were in turn supplanted by Burial Mound II and later (1200–1400 A.D.) by Temple Mound I and Temple Mound II cultures. Ford and Willey derived the Iroquois culture of New York from a welding of these four intrusions onto an archaic hunting-gathering population; they considered that this and other allied upper Mississippian cultures reached a peak after 1500 A.D., and lasted until historic times. Although other evidence has been presented in support of the idea that maize was a late arrival in eastern woodland cultures (Linton, 1924; Kroeber, 1939), from a botanical point of view the postulated time of arrival of maize in this area appears too recent. This impression is strengthened by consideration of the length of time the same type of maize was present in the Southwest.

Recent radiocarbon dating (Johnson, 1951) indicated that Mississippi valley and other eastern cultures were of greater antiquity than had previously been

thought. Johnson (1951) reported that Hopewell sites from Ohio and Illinois were about 1000 years older than had previously been estimated. The whole chronology of the Southeast has become unsettled because of radiocarbon dating results, but the presence of cultures in this area at earlier dates further strengthens the idea that maize is of greater antiquity than had been thought possible, and opens a way to minimize a long-standing inconsistency between archaeological and botanical evidence.

Since there was, as Ford and Willey (1941) and Waring and Holder (1945) pointed out, a suggestion of strong Mexican influence in Temple Mound I and II cultures, the idea would be greatly substantiated should remains of Mexican maize ultimately be found in excavations. Botanical evidence exists that maize of the Southeast is related to a Mexican Gulf Coast race (Wellhausen *et al*, 1951, 1952), and hybridization of this Mexican maize with eastern flint maize already present in the Southeast probably resulted in the variable forms called Southern Dents by Brown and Anderson (1948).

Northern Flint and Southern Dent maizes were subsequently brought together to form modern hybrid corn-belt maize (Anderson and Brown, 1952a, 1952b). A significantly large collection of Southern Dents was not available for inclusion in the present study, but the few available cobs which were studied showed a rather close resemblance to Northern Flints in cob characters. Evidence that many Southern Dents were intermixed with Northern Flints was presented by Brown (1949), who studied chromosome knob numbers in United States maize. He found Northern Flints to have the lowest knob numbers, Southern Dents the highest, and corn-belt forms intermediate between these extremes. Longley (1938) had previously surveyed Indian maize varieties from the United States and northern Mexico. He reported the same general rise in knob number among southeastern varieties. He also found that maize of Arizona and New Mexico was high in knob number. Carter (1949) used knob numbers on chromosomes of Indian maize to indicate tribal affinities and differences. The fact that such an investigation yielded results substantially the same as those of different approaches is another example of how closely maize mirrors the history of those with whom it is associated.

An important point regarding use of Northern Flint and Southern Dent maizes in corn-belt maize production is that the hybrid vigor manifest in this cross is based upon small differences between two already-intermixed races. This situation may possibly indicate that improvement of maize by hybridization techniques has barely begun. Since identification and classification of races are becoming a necessary part of maize breeding, a knowledge of cob variation should be of practical value in the development of new strains of hybrid maize. The principles of cob analysis set forth above, even though they employed small morphological differences, may be considered fundamentally sound, because results obtained from their analysis were in agreement with ethnological and archaeological as well as botanical data of other workers.

Summary

Morphological characters present in the female inflorescence, or cob, of *Zea Mays* L. have been measured on over 500 cobs representing both modern and archaeological varieties. External characters measured included row number, shank diameter, cob diameter, and over-all cob shape. Internal characters measured included cupule width, cupule depth, height of rachis-flaps, kernel thickness, lower glume width, rachis diameter, and pith diameter.

Analysis of pictorialized scatter diagrams of averaged measurements showed a high degree of association of these characters. These results agreed closely with those of previous investigations employing other methods. The results of archaeological maize analysis were in harmony with previous conclusions based on purely archaeological data. Such agreements indicate the validity of cob analysis for characterizing variation in races of maize.

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THE CYTOLOGY, MORPHOLOGY, AND SYSTEMATIC RELATIONSHIPS OF *DELPHINIUM* × *BELLADONNA* HORT. *EX* BERGM.*

MARILYN AMY GAGE

I. Introduction

Among the cultivated perennial Delphiniums the problem of the origin of the forms variously termed "garland larkspurs" (Bailey, 1930) or *Belladonna* types has been raised more than once. The group as it is known at present includes not only *Delphinium* × *Belladonna* Hort. *ex* Bergm., but at least the 45 variants listed by the Royal Horticultural Society (1949), and probably certain other hybrids of unknown origin some of which are no longer in cultivation but were recorded in the literature of the last century.

Two main theories have been proposed regarding the nature of the assemblage. (1) L. H. Bailey, following the example of Huth (1895), the last monographer of the genus, considered these plants to be forms of *D. cheilanthum* Fisch. var. *formosum;* his grounds are wholly morphological. (2) Lawrence (1936), on the other hand, has suggested that *D. Belladonna* originated in gardens as a triploid hybrid between a tetraploid species and a diploid species, and that subsequent doubling of the chromosome number resulted in the fertile line now in cultivation. His hypothesis is in line with the known facts, for until early in the present century *Belladonna* was quite sterile and was propagated wholly vegetatively; moreover, the present fertile strain is a hexaploid.

In studying the origin of cultigens the historical method alone is obviously inadequate. Students of cultivated plants are well acquainted with the hazards of attempting to place even well-known species into conventional taxonomic categories. Even with such a relatively recent variety as *D. Belladonna*, caution is necessary in considering historical references, for it often happens that opinions given in early descriptions are contradictory or suggest some parentage which, in the light of present knowledge of cytology and genetics, is far from the truth. One can accept, with caution, species listed in cultivation at a certain period, but there must always be the reservation that morphologically similar species are subject to confusion, and that any of these species may, and probably do, differ from their wild relatives as a result of horticultural "amelioration."

Morphological comparisons with known species have often been used in establishing the possible parentage of plants of unknown origin. This method is most useful in groups where there are clear-cut characters whose extreme and intermediate expressions are easily recognized. The genus *Delphinium* is, however, notoriously variable, and specific distinctions are based to a very great extent upon quantitative differences, such as width of leaf segments, degree of dissection of

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* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy. During the last year the study was carried out under a predoctoral fellowship of the National Science Foundation.

the leaves, extent and type of axial branching, degree of incision of the "bee", length of spur, and the like. Every one of these characters is subject not only to genetical, but also, to a high degree, to environmental variability. Therefore, before employing such characters, it is important to understand to what extent each character may be modified by the environment.

A third method of general use in establishing relationships between species, that of cytological analysis, is often more reliable. A number of investigators have shown that degree of relationship between species may often be estimated by studying the morphology and especially the pairing affinities of the chromosomes (see Stebbins, 1950, for a review of the literature). However, where the chromosomes of the parental genomes are not strongly differentiated there must often remain doubt as to the sources of the chromosomes which are pairing in the hybrid. Especially in polyploids above the tetraploid level such problems are intensified by the presence in the same individual of several genomes, so that autopolyploidy and allopolyploidy may coexist.

The relationships of *D. Belladonna* must therefore be considered from a combination of several standpoints, and the solution must be based upon that hypothesis which best makes use of the information obtained by each method.

Of the materials employed in this study, families of various species and hybrids were grown in the experimental greenhouses of the Missouri Botanical Garden and of Washington University, in St. Louis. Herbarium specimens were made available by the Bailey Hortorium of Cornell University and from the collections of the Missouri Botanical Garden.

I wish to acknowledge my indebtedness to Dr. G. A. L. Mehlquist, of the University of Connecticut, formerly Research Horticulturist at the Missouri Botanical Garden, who suggested this problem and who stimulated my interest in it by his own enthusiasm. I am also indebted to Dr. Edgar Anderson and other members of the staff of the Missouri Botanical Garden who have aided me in many ways.

II. Taxonomy and Morphology

A. NATURAL SPECIES

History of the Genus.—

Since the establishment of the genus in its modern form by Tournefort (1700), *Delphinium* has received various treatments. In his 'Species Plantarum' Linnaeus listed the six species, *D. consolida*, *D. ajacis*, *D. peregrinum*, *D. grandiflorum*, *D. elatum*, and *D. Staphisagria*. By the close of the eighteenth century only six more species had been added, but in the century and a half since then, the number of species described has increased to more than 300. A. P. DeCandolle was the author of 23 species, and in his 'Prodromus' (1824) he grouped 53 species into the four sections, CONSOLIDA, DELPHINELLUM, DELPHINASTRUM, and STAPHISAGRIA. K. Prantl, in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien' (1888) merged DeCandolle's STAPHISAGRIA and DELPHINASTRUM into one section, STAPHISAGRIA;

and later, modifications were made by others—notably Asa Gray (1887), Robinson and Fernald (1908), and Huth (1895). The most recent treatment of the American species is that of Ewan (1945).

Huth published in 1895 his "Monographie der Gattung *Delphinium*," in which he attempted a natural classification of the 200 odd species treated. He recognizes two subgenera: CONSOLIDA, in which there is a single carpel, the petals are fused into one, and seeds are scaled and three-cornered; and EUDELPHINIUM, in which there is more than one carpel and the four petals are free. Within the second subgenus he distinguishes three sections:

ELATOPSIS—petals deep violet or black, lower petals bifid and bearded.

DIEDROPETALA—petals light, the same color as the sepals or dirty yellow, deeply bifid, lobes acute.

KOLOBOPETALA—color of petals as in DIEDROPETALA; limb of lower petals round or rectangular, entire or bilobed, lobes round or truncate at tip.

Of the species considered here, *D. elatum* L. belongs to the series RACEMOSA of section ELATOPSIS, and *D. grandiflorum* L., *D. cheilanthum* Fisch. *ex* DC., and *D. tatsienense* Franch. are included in the series CHEILANTHOIDEA of section KOLOBOPETALA. While *D. Belladonna* Hort. was not known to Huth, he included as varieties of *D. cheilanthum* several cultigens which are certainly very similar to it.

Further consideration of the taxonomic categories will be restricted to *D. cheilanthum*, since it alone has been confused with *D. Belladonna*. The other species (*D. elatum*, *D. grandiflorum*, and *D. tatsienense*) are taxonomically well-known, and while they include many natural and horticultural variants, there is no problem in determining the affinity of such variants.

Delphinium cheilanthum Fisch. *ex* DC.—

Apart from the question of any direct relationship between *D. Belladonna* and *D. cheilanthum*, a problem which will be discussed later, the two species are confused in herbaria and in gardens, where identifications must be made largely upon a morphological basis. The magnitude of the problem is amply brought out by L. H. Bailey in 'The Garden of Larkspurs' (1939), in which he attempts to trace the history of *D. Belladonna* as a derivative of *D. cheilanthum*. He bases his conclusions upon a comparison of certain historic plates and descriptions of *D. cheilanthum* and of certain horticultural varieties (*D. formosum* Hort. and *D. Henderson* Hort.). The last two will be taken up in the next section, and I shall discuss here only *D. cheilanthum* in order to clarify its position, since it is apparently infrequent in herbaria in this country.[1]

Delphinium cheilanthum Fisch. *ex* DC. is based upon a specimen sent to A. P. De Candolle (1818) by Fischer from the region of Doroninsk in Dahuria (in

[1] Bailey (1939) says: "Yet it is strange that *cheilanthum* does not appear as a native plant in the great herbaria to which I have had access. Specimens cited by Huth mostly are plants considered by him to be botanical varieties of *D. cheilanthum*."

trans-Baikal Siberia). In 1819 von Schrank figured and described the same plant (under the name of *D. cheilanthes*) in 'Plantae Rariores Horti Academici Monacensis' (pl. 7). Earlier, in 1769, J. G. Gmelin had described and illustrated in his 'Flora Sibirica' a plant which, according to De Candolle, Fischer had indicated was the same as his *D. cheilanthum*. In 1820 a plant grown near London from seed sent by Fischer was figured in the 'Botanical Register.'

In addition to the sources cited by Bailey, a number of accounts of the species given by collectors in Siberia and northern China (Ledebour, 1842; Regel, 1861; Trautvetter, 1847, 1877a, 1877b; Turczaninow, 1842; Glehn, 1876; Brühl, 1896; and Komarov and Schischkin, 1937) delimit *D. cheilanthum* Fisch. as a species or species complex, with well-defined characters and a distinct geographic distribution. From these accounts, and the Huth monograph, the species may be characterized as follows:

Delphinium cheilanthum Fisch., in DC. Prodr. 1:53. 1824.—Stem tall, simple or branched; leaves glabrous or pubescent (especially on the under surfaces), 5-parted, parts oblong to narrowly lanceolate-acuminate; lower bracts many-parted. Inflorescence racemose to subcorymbose, peduncles bibracteolate; upper bractlets equal to spur. Flowers blue, rarely white; spur straight or slightly curved; sepals ovate, pubescent or puberulent externally; upper petals glabrous, pale yellow or blue, lower petals large, with ovate or subrotund limb, entire or rarely emarginate-bilobed, with yellow pubescence above. Carpels 3, glabrous or pubescent, tips curved at maturity, to 20–25 mm. long; seeds 3-angled, with winged margins, faces scarcely squamate. Flowers in June and July (pl. 9).

A number of varieties have been described, but undoubtedly any future monographer must rework the alliance. The exact limits of the species are still somewhat in question, since Huth describes *Delphinium Middendorffii* Trautv. as a distinct species, although in his natural key to the genus he lists it as a variety of *D. cheilanthum*, distinguished by having the apices of the sepals lanceolate. Moreover, he notes: "*D. Middendorffii* scheint eine verkümmerte Form des *Delphinium cheilanthum* mit verlängerten Kelchblättern zu sein." By 1877 Trautvetter, who originally described *D. Middendorffii* (1847), conceded that it was but another variety of *cheilanthum*, and added (translation):

> "*Delphinium cheilanthum* Fisch. varieties grade into one another and are distinguishable with difficulty. This species possesses sometimes a low stem (var. *Middendorffii*) and sometimes a taller stem; and this latter form has flowers either larger (var. *typica*) or smaller (var. *parviflora*). Indeed, sometimes var. *Middendorffii* has larger, and sometimes smaller flowers, so that sometimes it approaches var. *typica* and sometimes var. *parviflora*."

An American species, *D. chamissonis* Pritz. (from the Bering Sea region and the Yukon valley) is also apparently a close ally of *D. cheilanthum*. Comparing *D. chamissonis* and *D. Middendorffii*, Ewan (1945) says: "All of the more than a score of collections examined show so much variation in spur length and, indeed, flower size as a whole, as to render it difficult to draw any distinction between the two species from these characters."

B. HYBRIDS OF THE BELLADONNA TYPE

The history of the cultivated Delphiniums is extremely complex (see Wilde, 1931; Bailey, 1939). As early as 1778 *D. elatum* L. and another form listed as *D. azureum* (not *D. azureum* Michx., which was not described until 1803) were offered in the trade, and at least by 1824 *D. grandiflorum* L. (two varieties) was offered. Other species were rapidly introduced and by the middle of the century hybridization was being carried on by a number of French growers, chief among whom was Victor Lemoine, originator of most of the first varieties of perennial garden Delphiniums. English plantsmen were somewhat later in the field, but particularly since the 1870's, when the first varieties of James Kelway were introduced, a large part of the development of new hybrids has been carried out in Britain.

As nearly as can be ascertained, most of the present forms were derived from relatively few species. *D. grandiflorum* and *D. elatum* have chiefly been involved, although hybrids with other species, including *D. tatsienense* Franch. (Lemoine, 1914), *D. cardinale* Hook. (Wilde, 1931), and *D. nudicaule* Torr. and Gray (Lawrence, 1936) have enjoyed some popularity. Horticultural literature has frequently not been reliable regarding species in cultivation, and allies of *D. grandiflorum* or *D. elatum* could have been confused with these species and so have been employed in crosses at a time antedating any existing records of their use.

As has been mentioned above, *D. Belladonna* first appeared some time after the middle of the last century; the earliest known mention of its name is in 'Floricultural Cabinet and Florist's Magazine' for 1857, where it is listed as a desirable form with large pale lavender-blue flowers. In the 1865 catalogue of James Backhouse & Son, of York, England, *Belladonna* is listed and described as "a lovely turquoise, perfectly hardy." There are sporadic references to the plant in various horticultural publications before 1880, in which year the English firm of Kelway introduced it to a wide market. For a long time *Belladonna* was reported to be sterile. However, in 1902 or 1903 a plant grown by G. Gibson, of Leeming Bar, yielded three pods, whose seeds produced five plants, two of which became the named varieties "Mrs. G. Gibson," and "Grandiflora" (Phillips, 1949); and in 1905 Sutton & Sons, of Reading, England, obtained seed from two plants. Thus it appears that a chromosome-doubling occurred at least twice within a few year's time. The fertile strain has always been true-breeding, in the sense that there has been no recovery of anything which resembles any diploid or tetraploid species which might be assumed to have been the original parents (although it will be demonstrated later that weak but measurable associations of characters present in such species are still to be found). It it true, nonetheless, that heterozygosity in these original amphidiploid forms must have been fairly high, judging from the large number of *Belladonna* varieties introduced within the next few years.

It is of interest that the 'Journal of the Royal Horticultural Society' (1907) says of Sutton's first seedlings: "Some . . . resembled *Delphinium Belladonna* very closely, but some more nearly approached *Delphinium formosum*, and one bore

flowers of a very beautiful deep blue tint." *D. formosum* referred to here is the horticultural form and not the species of Boissier and Huet. Like *Belladonna*, it was a garden hybrid of unknown origin, and, also like *Belladonna*, it is said to be a hexaploid (Propach, 1939, 1940; Mehlquist, unpublished). It was first offered in 1855, and according to Van Houtte (1857) it was already fertile. This, coupled with its superficial resemblance to the diploid species *D. cheilanthum*, caused Huth to list it as a variety of that species in his monograph, although it has never been reported in nature (pl. 8). It is suggested that *formosum* may have originated from an early and unrecorded doubling of the chromosome complement of *Bella-*

Text-fig. 1. Leaf types in *Delphinium* species and hybrids (× ¼).
1. *D. grandiflorum* var. *chinensis* Blue Butterfly.
2. *D. grandiflorum* var. *chinensis*.
3. *D. tatsienense*.
4. *D. cheilanthum*, from specimen collected by Karo in Dahuria.
5. *D. cheilanthum*, from plant grown from seed at the Missouri Botanical Garden.
6–9. *D. elatum*, showing range of variation.
10–15. *Belladonna* types: 10, Lamartine; 11, Smith's *Belladonna*.
16–20. Experimentally produced triploids: 16, 50-15-3; 17, 50-40-2; 18, 48-27-4; 19, 48-27-6; 20, 48-27-10.

donna, or at any rate that it originated in the same manner as *Belladonna.* Certainly, there are no consistent differences between the two.

The following is a general description of *D. Belladonna:*

DELPHINIUM × BELLADONNA Hort. *ex* Bergm.[2]—Racemose open-flowered perennial with simple or branched stem up to 1.5–2.0 m. tall; herbage pubescent or glabrous; leaves palmate or deeply 3-parted and strongly ribbed, the parts again divided or lobed, the degree of dissection of the parts gradually increasing from rosette leaves to bracts, the main division of the stem leaves narrow-cuneate to narrow-oblong, 0.2–2.0 cm. broad at base, the petioles nearly or quite as long as the blade. Inflorescences of relatively short and open (5- to 20-flowered) racemes, the peduncles with parted bracts at base and the pedicels usually long, with basal simple bracts and paired short bracteoles immediately subtending the flowers. Flowers large, single, occasionally semi-double, mostly light to dark blue and somewhat declined; sepals thinly pubescent outside, blunt; spur about equalling the sepals and straight or somewhat curved at the end; petals mostly white or light-colored, bearded with yellow, making a large "bee" which fills the throat of the flower. Follicles 3, pubescent or glabrous, up to 2.0 cm. long, the apex curved; seeds 3-angled with somewhat winged margins, not squamate. Flowering period prolonged by the production of successive shoots during the growing season (pl. 8).

Another variety of interest, Lamartine, originated with the French house of Lemoine & Son in 1903. Like *Belladonna,* it was at first sterile, and the present fertile strain had its origin in 1916-17 when doubling of the chromosome number apparently occurred among some plants growing at the Royal Moerheim Nurseries in Holland (Lawrence, 1936). The parentage of this variety is also obscure. In answer to my inquiry, the present head of the firm replied that they had no record of its antecedents, but that experimental work had suggested that the parents might have been an *elatum* type (*sic,* Pacific Giant) and *D. grandiflorum.* In habit, Lamartine is quite similar to *Belladonna,* being of the same height, with a loose, tapering spike, and fairly numerous lateral branch spikes. The leaves are similarly cut (text-fig. 1). The flowers are long-spurred, with sepals ultramarine suffused with purple, and the petals are dark-edged, shading to white, with a yellow beard. Like *Belladonna,* it has an extended blooming period.

There are also grown at present two triploid varieties, *Moerheimi* and Capri, which, while not directly related to *Belladonna,* have a close morphological similarity to that variety. The most complete and authoritative account of these triploids is that given by B. Ruys of the Royal Moerheim Nurseries (1911):

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[2] *D. Belladonna* Hort. is equivalent to *D. Belladonna* Bergm., listed in 'Index Kewensis.' Bergmans, who published his binomial in 1925, is among those who believe the plant to have originated from a cross between *elatum* and *cheilanthum.* He lists no sources for his opinion.

> "For about twenty years I have been interested in white Delphiniums and have purchased all the light-colored novelties which I could obtain, with a view to crossing them with large-flowered, light-blue varieties of strong constitution . . . [A few years ago] I found in a batch of seedlings one plant with five spikes. Of these, two spikes bore pure white flowers, two bore blue flowers, and some parti-colored, half-blue, half-white flowers. Next year, when the five divided plants flowered, I noticed that two had only white flowers, two only blue flowers, and one plant had some flowers white and others blue, whilst still others were half white and half blue."

Both the white and the blue variety were propagated and marketed, the former under the name of *Moerheimi,* and the latter as Capri. Aside from the color, there is no single definitive character to separate these and *Belladonna,* although, as mentioned above, these varieties are triploid.

In addition to the present-day varieties of the *Belladonna* type, a study of the literature reveals that other hybrids of similar appearance were known in the last century, though they have now passed from cultivation. Because of their bearing upon the possible constitution of *D. Belladonna,* some of these early hybrids are described below:

The earliest recorded *Delphinium* hybrid was *Barlowii,* figured by Lindley in the 'Botanical Register' of 1837. The plant, from a nursery in Tooting, had been received from an establishment in Manchester, and was believed to be the result of a chance cross between *D. grandiflorum* L. and *D. elatum* L. It was reported to be a continuous bloomer. 'Paxton's Magazine' described it the following year:

> "Plant perennial, growing usually from 4–5 feet high. Leaves with 5 principal divisions, deeply lobed and jagged; serrations acute; deep green on surface, light green beneath, smooth. Flowers semi-double, of a most intense blue color, produced very numerously in terminal spikes. Sepals of the calyx greenish externally."

Neither the description nor the Lindley plate, which shows a rather dense spike of semi-double blooms and, in the background, part of a leaf in outline, is complete enough to indicate the affinities of this plant. Moreover, except that the flowers are semi-double in each case, the Lindley plate is quite different from the Paxton plate, which indicates that the plant had a brownish bee, and leaves more deeply incised than those in the earlier plate. Since both plates were drawn from living plants, one is confronted with the alternatives that *Barlowii* was a highly variable variety, or that the two artists had available two quite different varieties. The plant in the earlier illustration might easily belong to the group of hybrids which includes *Belladonna;* the later plate appears, rather, to be merely that of an *elatum* variety. Herbarium specimens of plants sold as *Barlowii* within the last 20 years or so are quite different from either of these, being single dark-blue types, and not different morphologically from *D. Belladonna.*

The next form of interest, *D. Hendersonii* Hort. (pl. 7) is of extremely dubious background. It was first mentioned by Moore and Ayres in the 'Gardeners' Magazine of Botany' (1850) and was described under the name *D. cheilanthum* var. *Hendersonii* A. Henfr.:

"Hardy herbaceous perennial with large showy rather distant flowers. Leaves five-parted, lobes oblong or acuminated, trifid or obscurely bi-trifid, 4 inches in diameter, on long petioles; floral leaves three parted, with the lobes broadly linear, acuminated, simple. Racemes axillary and terminal, lax; the pedicels larger than the bracts. Flowers large and showy, ultramarine blue, with veins a little deeper; two lower petals with a roundish ovate limb, obliquely inflexed and whitish in the middle, bearing a yellow beard, slightly irregular on the margins, with a few ciliary hairs at the apex. Ovaries 3, glabrous, green, veined with bluish lines."

The text states that the plant was grown by E. G. Henderson of St. John's Wood, from seedlings purchased from M. Chauvière of Paris.

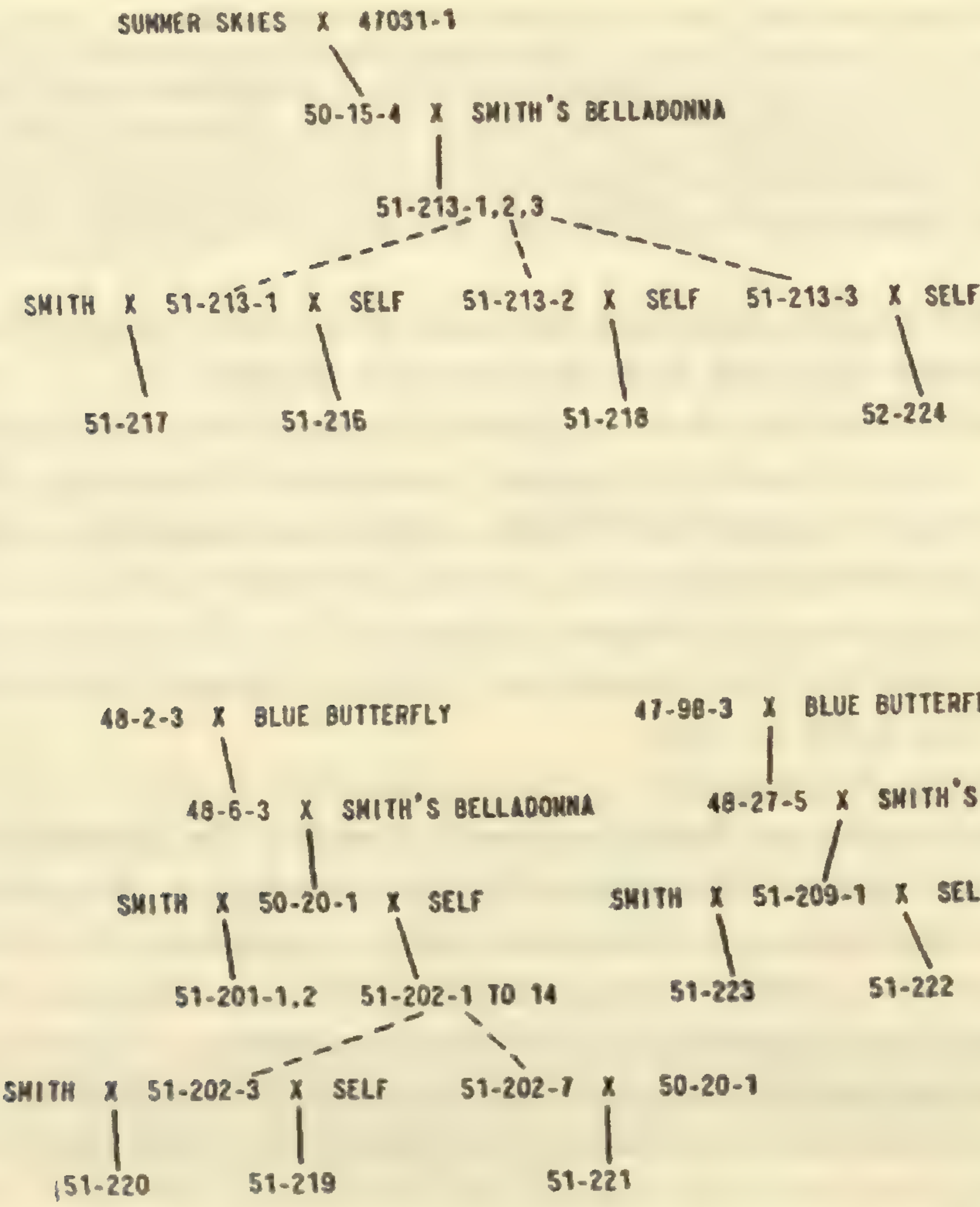
Lemaire's 'Jardin Fleuriste', of 1851, figures the same plant as *D. cheilanthum* var. *Chauvieri*. Lemaire regarded it as merely a variant of the species, whose distribution and habitat he considered briefly. Quite in opposition to Lemaire, Harrison (1853), describing the same plant, stated: "It was raised by M. Chauvière, nurseryman of Paris, from *D. chinense*, impregnated by *D. elatum-splendens*." This author also noted that *Hendersonii* was a profuse bloomer, of bushy habit, flowering over a long period of time.

Hybrids of known parentage.—

During the past eight years there have been produced at the Missouri Botanical Garden a number of hybrid Delphiniums of particular interest. Several hundred pollinations were made between *D. elatum* and different strains of *D. cheilanthum* and *D. grandiflorum* var. *chinense*, in an effort to find out which, if either, of these hybrids more closely resembled the *Belladonna* assemblage. Up to this time there have been no successful pollinations of *D. elatum* by *D. cheilanthum*. However, the other cross (that between *elatum* and *grandiflorum*) has been successful four times, yielding two families of 3 plants each, one family of 2 plants, and one family of 13 plants.

1. *47-98-3* × *D. grandiflorum* var. *chinense* "Blue Butterfly".—Hybrid Nos. 48-27-1 through 13. (This and the following cross were made by Dr. G. A. L. Mehlquist.)

The seed parent was one of a line of white semi-double *elatum* forms developed by Dr. G. A. L. Mehlquist. The group is exceptional in being the only line of whites in which there has been an approach to homozygosity without concomitant weakening and loss of the line. 47-98-3 had dense spikes borne on the rather short main axes, and leaves of medium size, pubescent, and palmately divided, with relatively narrow segments (pl. 10). The pollen parent, on the other hand, was a low-growing plant with a branched, very open inflorescence of fairly large rich deep blue single flowers in few-flowered panicles. The leaves were relatively small, dull green, glabrous, and finely dissected. This form, too, was true-breeding, and the variety has been grown at least since 1910 when it was among the perennials planted at Wisley (Jour. Roy. Hort. Soc., 1910) (pl. 9 and text-fig. 1). The progeny of this cross included 13 individuals which were generally of intermediate habit and varied very little among themselves. The following description serves to characterize them and point out their chief differences from the parents.



Text-fig. 2. Pedigrees of major lines of triploids and hexaploids.

48-27- Series.—Racemose open-flowered perennials, with simple or usually branched stem up to 1.0–1.25 meters tall; herbage pubescent. Leaves palmate and deeply 5- or 3-parted and strongly ribbed, the parts again divided or lobed, the degree of dissection increasing progressively from the rosette to the bracts, the main divisions chiefly narrow-cuneate, up to about 1.0 cm. broad, the petioles as long as or slightly longer than the blade. Inflorescences not spiciform, the terminal one a 15- to 20-flowered raceme, the lateral of fewer flowers, the peduncles with 3-partite bracts at base and the pedicels with basal simple bracts, and paired bracteoles 0.8–1.0 cm. long subtending the flower. Flowers medium-sized, single, violet and cobalt, on long pedicels and somewhat declined; sepals thinly pubescent outside, blunt, the spur slightly longer than the limb and usually somewhat curved at the end; petals the same color as the sepals, bearded with short golden yellow hairs. Follicles 3, pubescent, not developing into fruits, apex curved. Flowering period prolonged by the production of successive shoots during the growing season (pl. 11 and text-fig. 1).

2. *48-2-3 × Blue Butterfly.*—Hybrid Nos. 48-6-1 through 48-6-3.

48-2-3, the seed parent of this group, was a selection from Vetterle and Reinelt's

Galahad Series of their Pacific Giant Hybrids. The plant, a white semi-double, was not available to me.

The three hybrid individuals in this group were quite similar to the hybrids described above, the chief differences being the regular production of one or several additional petals of either sort, and the generally larger, less open flowers.

3. *Summer Skies* × *D. grandiflorum (47031-1)*.—Hybrid Nos. 50-15-1,-3,-4.

The seed parent of this cross is a selected seedling from the Pacific Giant series, Summer Skies, an *elatum* type with semi-double flowers with sky-blue sepals and white petals in tapering, somewhat dense spikes (pl. 12). It has been found to be true-breeding for color (Mehlquist, unpublished). The pollen parent was from seed obtained from the Royal Botanic Gardens at Kew as *D. tatsienense*. However, determination of the plant, using Huth's key, showed that it must have been, rather, a corymbose variety of *D. grandiflorum*. Numerous attempts were made to obtain seed, but 47031-1 was completely seed-sterile.

The three hybrid individuals of this cross differ in a number of particulars from those of the other crosses, being taller, with a strong main axis which bears lateral spikes in the manner of *D. elatum*, but these more profuse and more strongly developed than in that species. Leaves of 50-15-3 are much like those of the 48-27- series, whereas those of the other two plants are considerably larger and have the ultimate divisions rounded rather than acute. The flowers are again mixed blue and violet (although the blue of these plants is somewhat more brilliant than in the other crosses) and are more or less semi-double, with spurs about ⅕ longer than the standard of the sepal (pl. 12, and text-fig. 1).

4. *47-98-3* × *47031-1*.—Hybrid Nos. 50-40-1 and 2.

The seed parent was the white *elatum* used in producing the triploids of line 48-27; the pollen parent was also used to produce the triploids of line 50-15. The two individuals of this cross resembled those of 48-27, except that the leaves were more finely dissected, and the flower was the same brilliant cobalt noted in the 50-15 individuals (text-fig. 1).

5. *Derived hexaploid hybrids*.—

Since the fertile strain of *D. Belladonna* apparently originated from spikes whose chromosome numbers had been fortuitously doubled, it was hoped that it might be possible to produce doubling of the chromosomes of the hybrids described above. With this in view the developing rosettes were treated each year for three years with aqueous colchicine in various concentrations for varying lengths of time. In at least one case, doubling of the somatic chromosome number of the spike was achieved, judging not only from morphological features but from greatly increased amounts of "viable" pollen produced (Table I), but the 14 seeds obtained did not germinate.[3] The other method employed, that of repeated selfing

[3] It is not known whether delayed planting or some undetermined genetic factors may have been the cause of the failure to germinate—certainly, one of the chief problems in the growing of *Delphinium* is storage of the seeds. Lots which have germinated well when planted immediately may not germinate at all after six months, even in cold storage.

TABLE I

POLLEN SIZE AND VIABILITY IN SPECIES AND HYBRIDS OF *DELPHINIUM*: LIVING PLANTS.

Plant	% Viable pollen	Pollen diameter in μ	
		Range	Median
Diploids			
D. grandiflorum			
Blue Butterfly	97.0	18.8–37.6	23.5
47031-1	65.0	18.8–28.2	23.5
Tom Thumb	91.0	23.5–37.5	28.2
D. cheilanthum	98.0	23.5–32.9	28.2
Tetraploids			
47-98-3	64.6	23.5–37.5	30.6
Summer Skies	32.0	23.5–37.6	30.6
Triploids			
48-6-1	5.7	28.2–37.5	32.9
48-6-2	7.0	23.5–40.0	32.9
48-27-1	16.0	25.9–40.0	30.6
48-27-3	14.0	23.5–37.6	32.9
48-27-4	6.0	21.2–47.0	35.3
48-27-5	21.0	23.5–42.3	32.9
48-27-6	3.2	23.5–37.6	35.3
48-27-7	9.0	23.5–36.5	32.9
48-27-8	4.0	23.5–42.3	32.9
48-27-10	16.3	21.2–51.7	37.6
48-27-11	5.0	23.5–37.6	30.6
48-27-12	2.7	23.5–47.0	32.9
50-15-1	1.5		
50-15-3	0.0		
50-15-4	2.5		
50-40-2 (untreated)	2.0	21.2–37.6	30.6
50-40-2 (treated)	52.0	25.9–37.6	30.6
Moerheimi	0.5		
Hexaploids			
Smith's *Belladonna*	41.0–95.0	23.5–42.3	32.9
Cliveden Beauty			
-1	68.2	30.6–44.7	37.6
-5	80.5	25.9–37.6	32.9
Lamartine	82.5	23.5–32.9	30.6

of the triploids, proved even less satisfactory, only two inviable seeds being produced from upwards of a thousand individual pollinations made in several seasons. However, pollinations of the triploids by *Belladonna* proved more successful: eventually ten plants, representing five crosses, were obtained, and of these, five plants (representing three crosses) were used in establishing new hexaploid lines, both by selfing and by backcrossing to *Belladonna*. A detailed description of the cytology of these hybrids follows (chapter IV), but it is to be noted that in morphological characters and cytological details they do not deviate from

the *Belladonna* category except in being more variable; and in some cases fertility is already as high as in *Belladonna*.

C. DISCUSSION

Two major points are to be brought out here: First, while it has been demonstrated that there is indeed a resemblance between the Asiatic diploid species *D. cheilanthum* Fisch. *ex* DC. and the hexaploid cultigen, *D. Belladonna*, there are also important differences. The botanical species and its allies are restricted to Siberia, Mongolia, and North China, and to the islands of the Bering Sea and the Yukon, and it has not often been planted in gardens. Moreover, when one comes to compare the two entities, the first impression of similarity is modified by an appreciation of their subtle differences. Thus, the leaf of *D. cheilanthum* may often be incised so that the major divisions are of about the same width and degree of segmentation as in the Belladonnas, yet the latter will invariably have the ultimate divisions more acuminate, the segments often intricate, and the main lateral veins divergent in their departure, features rarely present in *D. cheilanthum*, and certainly never present in combination in that species. The flowers of *D. cheilanthum* are small but always have an extremely conspicuous bee; while the bee of *Belladonna* may be of the same absolute size, it is always smaller in proportion to the size of the flower. Lastly (and it is realized that the botanist will not often have access to the quantity of material necessary to make this distinction), if one has on hand a number of plants of both sorts, it is a relatively simple matter to separate the Belladonnas from *D. cheilanthum*, since the latter holds together by virtue of concordant variation, and the former is less cohesive on account of discordant variation (Anderson, 1951).

The second point brought out in this section is that *Belladonna* types have originated a number of times in the past, and always they have first been noted in gardens. From the evidence, it seems clear that *Hendersoni*, Lamartine, *Moerheimi*, and the others, while not directly related, are quite similar in leaf shape, flowers, branching habit, and prolonged blooming periods. Several of them reproduce by seeds; others have been completely sterile. In no case has the exact origin of the plant been unquestioned. However, all of them have been found to be very much like certain hybrids produced by crossing *Delphinium elatum* and *D. grandiflorum* varieties. In the absence of direct evidence one cannot immediately exclude *D. cheilanthum* as one of the parents, but evidence against such a supposition will be given in the following pages.

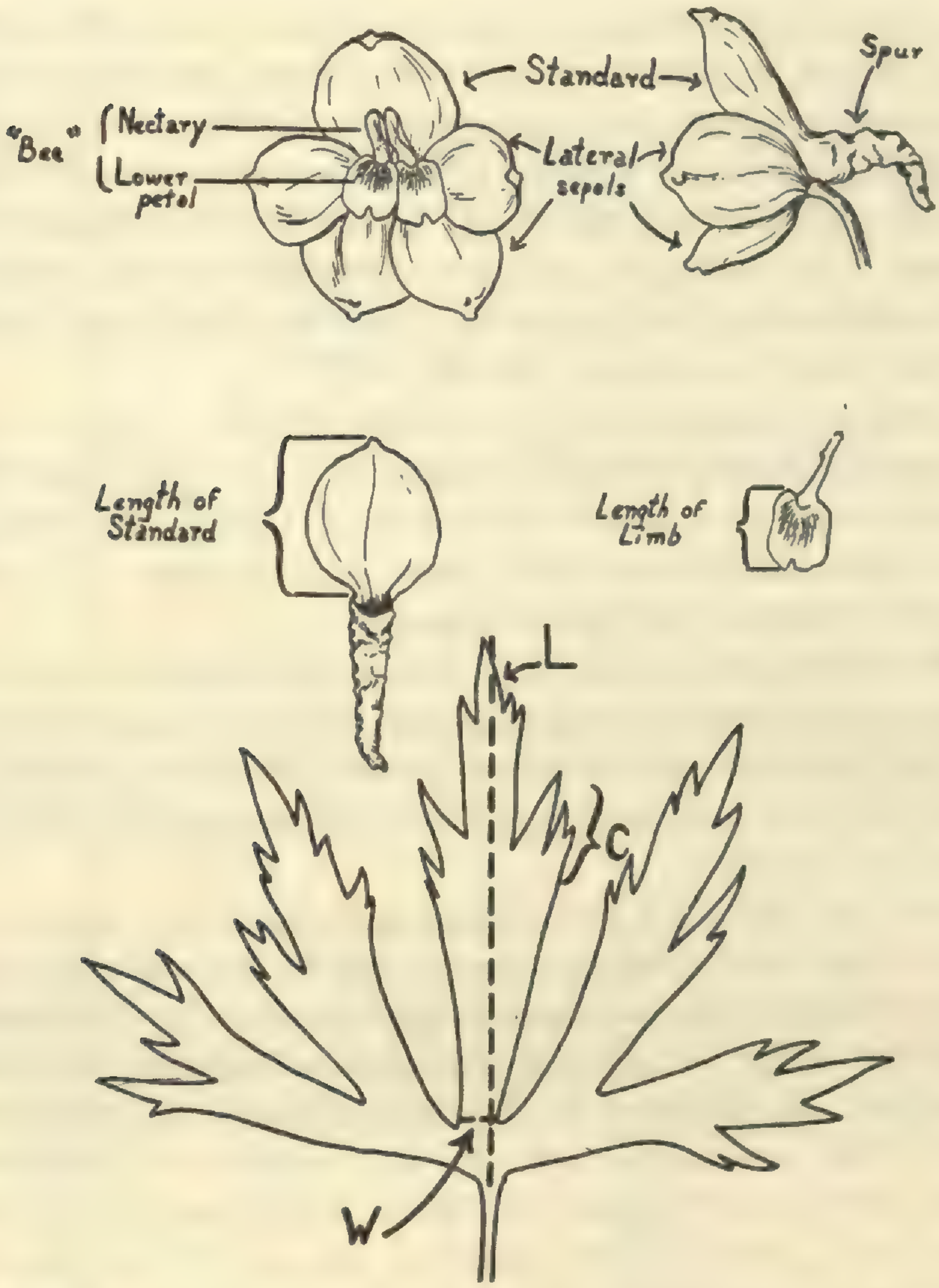
III. Character Association as an Aid in Establishing Relationships

At least since the time of Gmelin, botanists faced with the necessity of classifying species of *Delphinium* have realized the difficulty of finding reliable specific characters. This is the result not so much of lack of genetic differentiation within the genus, as of the presence of numerous characters of a quantitative nature,

whose genetic basis may be modified or simulated by environmental factors. On account of this "inability to use one or two *differentiae* to distinguish species or subspecies," Ewan (1945) has based his treatment of the North American species on "maximum correlation of characters existing in combinations." A species characterized in such terms could be visualized, then, as a plexus of "typical" individuals, possessing the most pronounced correlation of the characters of the species, and a large number of individuals possessing these characters in lesser degree, but with no sharp discontinuities within the group. Such discontinuities, on the other hand, would be expected between species; and populations of hybrid origin might be expected to be largely coherent, but with some segregation if the parental genomes have sufficient segments in common that occasional heterogenetic pairing occurs (chap. IV).

The study of hybrid ancestry in such a group as this would not long ago have been considered a very difficult one from which to arrive at any very definite conclusions. However, the student of variation has been given a valuable tool in the graphic methods developed by Anderson (Anderson, 1948, '51, '52; Anderson and Gage, 1952), which permit the study of complex patterns of variation on the two-dimensional level of the scatter diagram and ideograph. As Stebbins (1952) has recently pointed out, the method of extrapolated correlates involves more than the mere random choice of characters; rather, the choice of a measure is determined by how well it expresses a feature of the plant, and how subject that feature is to environmental variation. While the methods are thus a compromise between pure statistical analysis and subjective intuition, their success in a number of cases indicates their great usefulness.

Before employing these methods in *Delphinium*, it was necessary to study thoroughly within-a-plant variation. Good material for such a study was available in pressed material, and in living plants of several vegetatively propagated individuals, chiefly hybrids of the 48-27 and 50-40 series and Smith's *Belladonna*. Preliminary measurements of a number of characters demonstrated what was already suspected, that only a few features of the leaf could be used. (Leaf variation in *Delphinium* has been the subject of various investigations: Brown, 1944; Lewis, 1947; Ashby, 1948.) By trial and error it was eventually possible to score a number of characters which exhibited low variation even on divisions of a plant grown in different years. In addition to the few leaf characters, those characters most effective for measurement were those of the flowers and inflorescence. (Certain definitive characters, such as internode pattern, mode of branching, etc. could not be employed because of the scanty amount of herbarium material.) With these measurable characters as guides, the three natural species (*D. elatum*, *D. grandiflorum*, and *D. cheilanthum*) and *Belladonna* were studied, and those features which could be used alone or in combinations as differential characters were selected for use in separating the units on a multiple-character basis. The characters used were the following:



Text-fig. 3. Floral and leaf characters used in constructing scatter diagrams.

Leaf.—

Length of median segment/length of *C* (text-fig. 3). Since both measures are about equally dependent on absolute size of leaf, their ratio expresses fairly well the depth of cutting of the segments.

Width of median segment.—

This was found to be the best measure expressing what may be termed the degree of dissection of the segments.

Inflorescence.—

Number of flowers. The absolute number of flowers on the main axis was used.

Density. This was computed as the length of the inflorescence in inches (measured from the attachment of the lowest flower on the main axis) divided by the number of flowers.

Flower.—

Margin of bee. Scored in three grades: bifid, notched, and entire or emarginate.

Length of standard divided by length of limb of the bee (text-fig. 3).

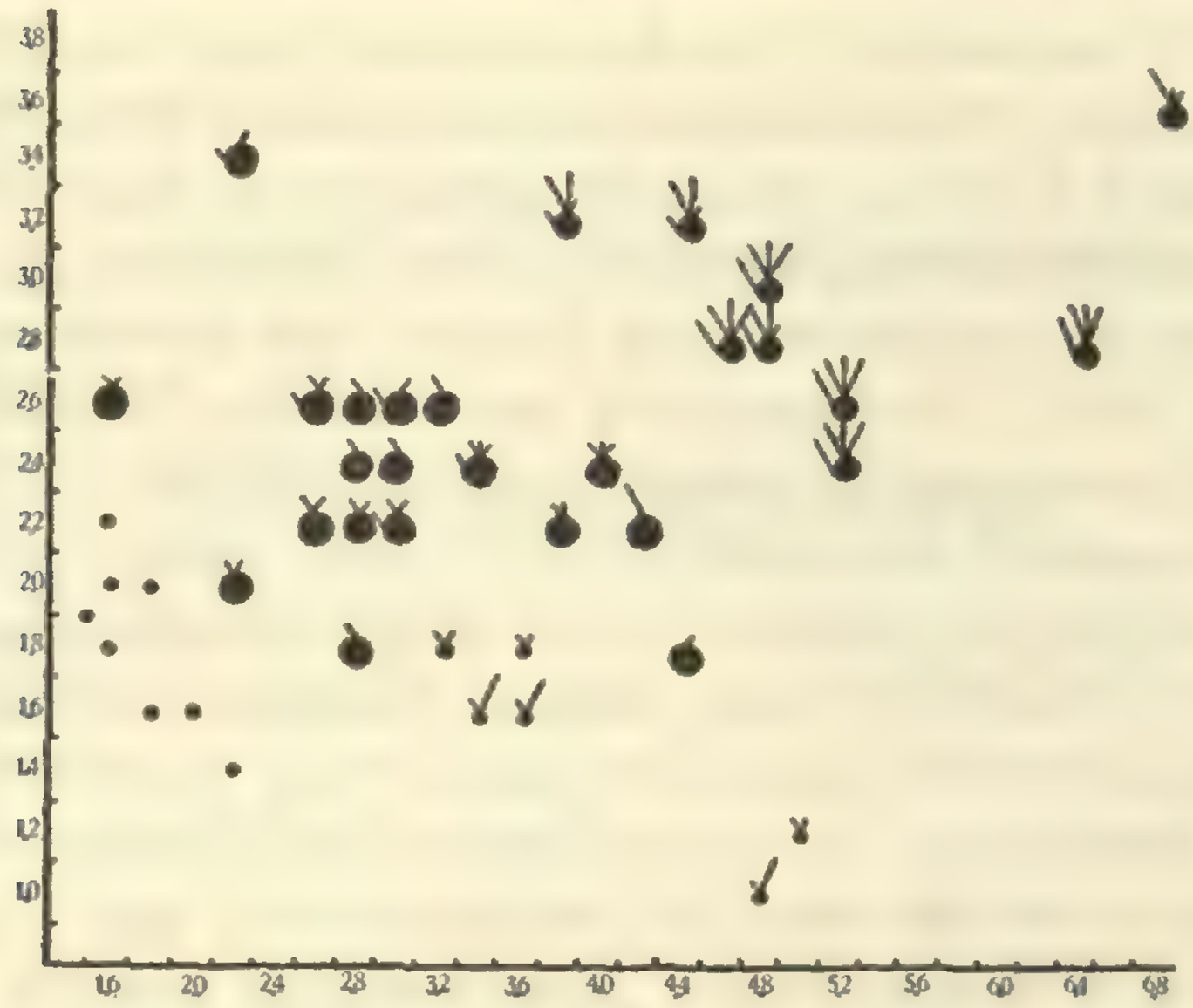
In laying out the scatter diagram (text-fig. 4), the ratios used as ordinate and abscissa were selected because, varying widely among the plants measured and expressed as individual grades, they permit a wide scattering of the points on the diagram. Moreover, the use of measures of one floral character and one leaf character lessens the possibility that they might be merely different manifestations of the same factor. The scoring of the other characters was then adjusted so that each could be expressed in three grades, to which ray lengths and positions were assigned (further details accompany text-fig. 5).

The "population" represented by the scatter diagram consists of herbarium specimens from the Missouri Botanical Garden and from the large collection of cultivated Delphiniums at the Bailey Hortorium of Cornell University. Extreme types such as double varieties and dwarf forms were excluded. All other measurable sheets were included in making the diagrams.

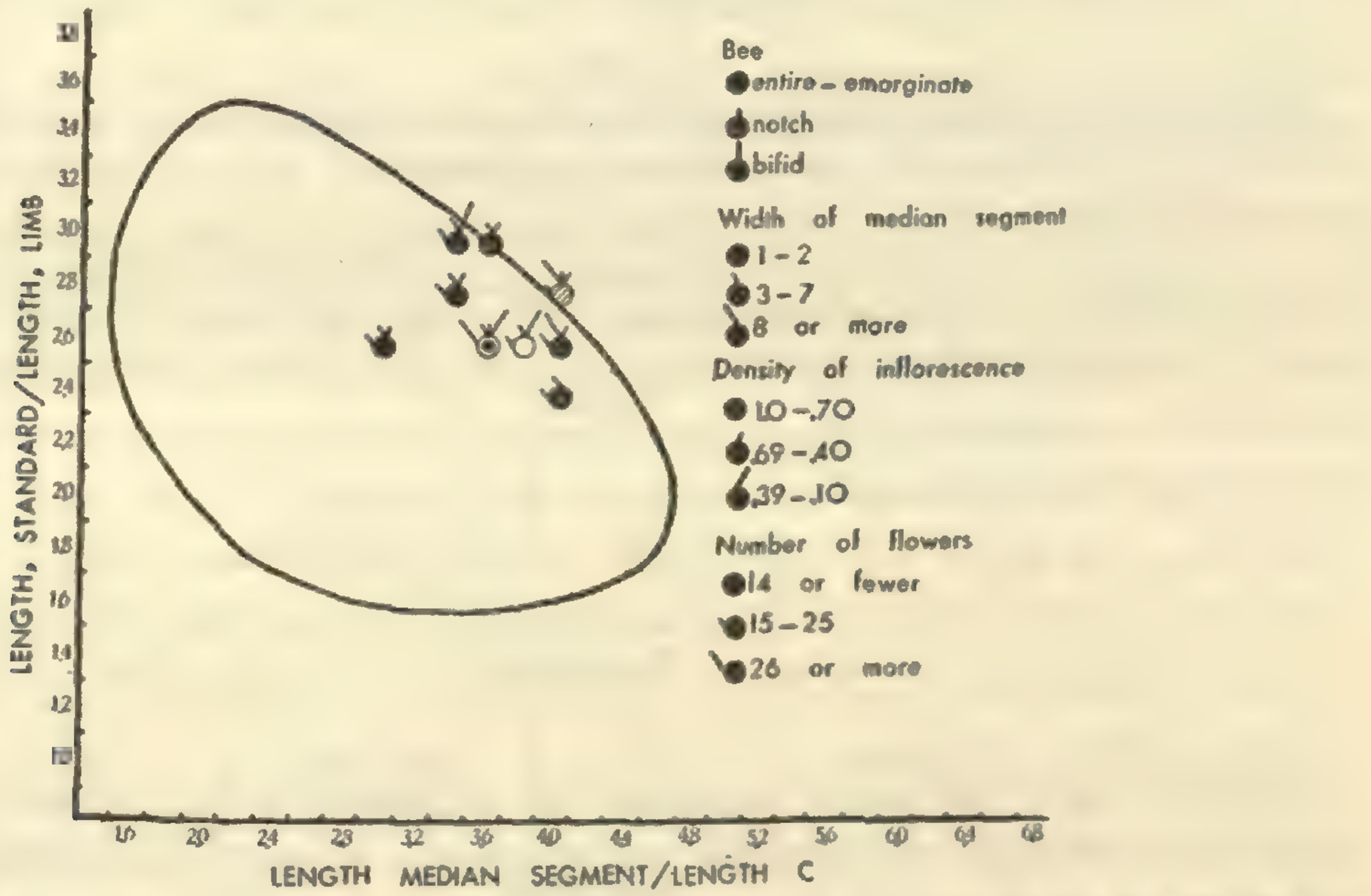
Since pollen measurements made from herbarium specimens were found to be reliable indicators of approximate polyploid level (chap. IV), an additional measure, determined by pollen grain size, is expressed by the size of the dots on the scatter-diagram, the smallest dots representing diploids, the intermediate dots, tetraploids, and the large dots, hexaploids.

A survey of the individuals thus diagrammed shows two distinct entities, *D. grandiflorum* in the lower left-hand corner, and *D. elatum* in the upper right-hand corner. Occupying the area between these species is the *Belladonna* complex, more variable than either but generally intermediate between the diploid and the tetraploid species. The position of *D. cheilanthum* just off the spindle but adjacent to *Belladonna* points out its notorious superficial similarity to *Belladonna*, but its actual physical distinctness is shown first by its diploid nature, and second by its almost "all or none" character with respect to the rays. It is seen to be not an intermediate between *grandiflorum* and *elatum*, but, rather, it possesses some characters in common with *grandiflorum* and some with *elatum*. (The plants of *cheilanthum* scored included two collections of two plants each, as well as two plants growing in the greenhouse at the Missouri Botanical Garden, and so shows more grouping of the dots than would a random selection.)

A graphic analysis of another sort, the internode diagram (text-fig. 6), points out clearly the differences in habit of the entities studied. Both *D. elatum* and *D. cheilanthum* have a relatively large number of nodes before the axis begins to branch; these increase somewhat in length from the highly shortened internodes of the rosette (not illustrated) but do not increase in a regular pattern and are generally not more than 7–8 cm. long. For *D. elatum* this was true not only of the cultigens, but of the wild species as well, where even dwarf alpine plants have a high node number, only the length of the internodes being shortened. In branching pattern these species may also be compared. On the whole (the exception being some garden types which are bred for a diffuse habit) side branches are few and much shorter than the main raceme which they subtend, generally decreasing in length from the lowest to the uppermost. The most evident distinction between



Text-fig. 4. Scatter diagram showing character correlations in *Delphinium grandiflorum* (small dots, rayless), *D. cheilanthum* (small dots, rayed), *D. elatum* (intermediate dots), and *D.* × *Belladonna* Hort. (large dots).



Text-fig. 5. Scatter diagram showing character correlations in members of the 4 triploid populations of this study. Distribution of *D. Belladonna* in outline.

these species, on the basis of habit, is that the inflorescences of *D. elatum* are relatively more highly compressed than those of *D. cheilanthum*.

The habit of *D. grandiflorum* is quite distinctive. Its nodal pattern is typically one of successively increasing internode length from the basal to the sixth rosette, the internodes reaching their maximum length usually by the sixth, and then becoming successively shorter through the inflorescence. While occasional varieties may branch very little, characteristically the plant is much-branched, the branches sometimes being placed at such an angle and being of such a length as to have the superficial appearance of dichotomies. (This is especially true in the closely

related species, *D. tatsienense*.) The branches may again branch in a similar manner (not figured). The maximum internode length in these relatively dwarf plants ranges from 5 to 18 cm., the higher numbers being quite common.

Variability in habit is characteristic of hybrid populations, as Anderson has repeatedly pointed out (see, for example, Anderson and Schregardus, 1944; Anderson and Gage, 1952). In allopolyploids such variability should be small if the variety is of the type termed by Stebbins a true allopolyploid (1947, 1950). If however, it is a segmental allopolyploid, more frequent pairing between members of the different genomes will result in a higher amount of segregation. *Belladonna* does, in fact, vary somewhat in habit, although the general tendency is for these plants to possess a more or less regular internode pattern, with branching common below the main inflorescence. In extreme cases the node number may be low, as in *D. grandiflorum*, and the aspect of pseudodichotomies may be found in the branching pattern; or they may be tall plants with short branches and internode lengths irregular below the inflorescence. On the whole, the direction of variation in this respect tends to be more toward *D. grandiflorum* than toward *D. elatum*.

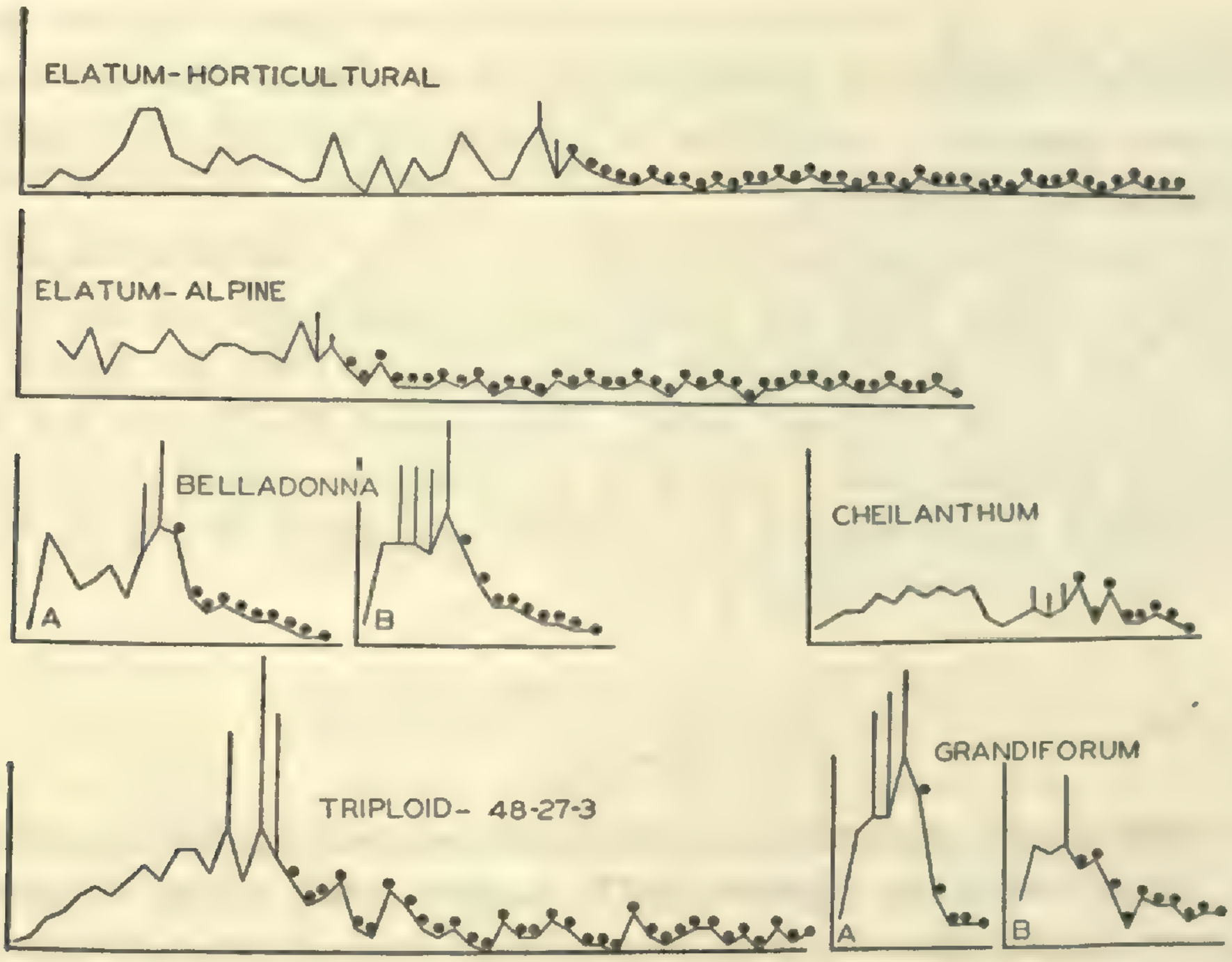
TABLE II

POLLEN SIZE AND VIABILITY IN SPECIES AND HYBRIDS OF *DELPHINIUM*: HERBARIUM SPECIMENS.*

Plant	% Viable pollen	Pollen diameter in μ	
		Range	Median
Diploids			
D. grandiflorum, Vilmorin-Andrieux	98	20.0–25.0	22.5
Blue Butterfly	96	17.5–25.0	22.5
D. cheilanthum, coll. Karo	92	20.0–25.0	20.0
Tetraploids			
D. elatum, Bot. Gard., Cambridge	98	22.5–25.0	25.0
D. elatum, King of the Blues	60	22.5–25.0	25.0
Hexaploids			
D. formosum Hort., N 71860	60	25.0–32.5	30.0
D. formosum Hort., Helms. 17/6/25	25	25.0–32.5	27.5
D. formosum Hort., Dreer, July 1924	50	22.5–32.5	30.0
D. formosum Hort., Fordhook	80	22.5–32.5	30.0
D. Barlowii Hort.†	77	22.5–35.0	30.0
D. Barlowii, Aug. 1†	31	22.5–32.5	30.0
Lamartine, Aug. 20	79	25.0–32.5	30.0

*Specimens listed are in the herbarium of the Bailey Hortorium, Cornell University.

†The confusion as to the identity of *D. Barlowii* has been discussed on page 120. The specimens cited here are morphologically of the *Belladonna* sort.



Text-fig. 6. Internode diagrams to scale of diploid, tetraploid, and hexaploid Delphiniums. Ordinate, length of internode; abscissa, number of internode from rosette. Upright lines represent branches and are drawn to a scale ⅕ that employed for internodes. The black dots represent single flowers.

Text-fig. 5 is a scatter diagram for such of the triploids as were adequately represented by living or herbarium material, and an internode diagram of a typical triploid is shown in text-fig. 6. From the superimposed silhouette of the *Belladonna* distribution (fig. 5) all these plants are seen to be within the limits of that group, or to be intermediate between *D. Belladonna* and *D. elatum*. The same observation is borne out by the internode diagram, which shows the internode pattern of *Belladonna*, but with the high node number more characteristic of *D. elatum*.

Summary.—Through the medium of the scatter diagram it has been demonstrated that *Belladonna* may be visualized as a more-or-less variable group, intermediate between the diploid *D. grandiflorum (vel aff.)* and the tetraploid *D. elatum*, and having as the source of its variation the segregation of characters derived from these species. Further, the experimentally produced hybrids between *D. elatum* and *D. grandiflorum* have been shown to be very similar to *Belladonna*, deviating from it only in characters for which their *D. elatum* parents were extreme. The scatter diagram also amplifies the position of *D. cheilanthum:* it is instantly differentiated from *D. Belladonna* by its diploid constitution, and by constant morphological characters.

The same conclusion is supported by the internode diagrams: there is a greater amount of variability in *D. Belladonna* (extreme types were diagrammed, but are

not included in text-fig. 6) than in the three natural species, but on the whole it is intermediate between *D. grandiflorum* and *D. elatum*. In this respect *D. cheilanthum* is closer to *D. elatum* than to any other entity, differing chiefly in the development of its inflorescence.

On the basis of character association, then, it is to be concluded that *D. grandiflorum* and *D. elatum* fulfill the morphological requirements for the parents of *Belladonna;* but that *D. cheilanthum* could not have been the diploid parent, given *D. elatum* as the tetraploid parent. One cannot thereby rule out the possibility that a tetraploid species other than *D. elatum* was involved, but no other known tetraploid species possesses the required combination of characters, nor is any other tetraploid so commonly grown.

IV. Cytology of Delphinium

HISTORY

The chromosome complement of *Delphinium* has been studied by a number of workers (Hocquette, 1922; Tjebbes, 1927; Langlet, 1927, 1932; Tischler, 1927; Beckman, 1928; Lewitsky, 1931; Lawrence, 1936; Propach, 1939, 1940; Gregory, 1941; Mehlquist *et al*, 1943, and unpublished; Lewis *et al*, 1947; and Lewis and Epling, 1951), and it has now been generally established that the basic complement of the genus consists of one long chromosome with a median centromere, one long chromosome with a sub-median centromere, five medium-length chromosomes with sub-terminal centromeres, and one short chromosome with a sub-terminal centromere. Langlet (1932) reported that satellites occurred in the genus, but his results were not conclusive regarding their number and location. Lewitsky (1931) published some data regarding chromosome differentiation within the genus, and furnished ideograms for a number of species. Noting that in certain instances the four "homologous" chromosomes are not identical, he postulated amphidiploid origin for two tetraploid species, *D. azureum*[4] and *D. elatum*. Moreover, he pointed out that two species belonging to two distinct sections of the genus, *D. cardiopetalum* and *D. Staphisagria*, have distinct types of ideograms from the other species he investigated. More recently, Lewis, Epling, Mehlquist and Wyckoff (1951), reported that the chromosomes of the California species of *Delphinium* (which according to Ewan (1945) include representatives of several of the Old World lines as well as a majority of endemics of uncertain affinities) are morphologically quite similar. They figure a composite ideogram from species included in Ewan's SPICIFORM series, which shows one satellited chromosome (their *E*, which they report is otherwise very close in length to *C*, *D*, and *F*). That the situation is not so simple as this and that greater possibilities exist for identifying different chromosomes in certain cases have been made clear from the present study in which, apparently for the first time in *Delphinium*, Feulgen and aceto-lacmoid squashes have been employed for somatic material.

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[4] *D. azurem* of Lewitsky was probably *D. elatum;* see footnote p. 164.

Numbers of chromosomes published so far in *Delphinium* are listed in the Appendix. Diploid species are by far the most numerous, tetraploids are occasional, and hexaploids are known only in cultivated forms.

Meiotic studies of *Delphinium* have been largely confined to the garden forms, the major exception being the work reported by Lewis, Epling, Mehlquist, and Wyckoff on the California species, where both diploids and tetraploids were analyzed. For the diploid species, metaphase bivalents fall into several easily recognized types, since terminalization regularly occurs and chiasma frequency for a given pair shows little variation, the large chromosomes having usually two chiasmata at metaphase (there may be three or rarely four at diplotene and diakinesis) and the others having regularly one chiasma only, and that in the longer arm (Mehlquist *et al*, 1943; Lewis *et al*, 1951).

In the tetraploids, the type of pairing varies, depending upon the origin of the tetraploid condition. Thus, in the California tetraploids, which are designated as races of the diploid species, *D. Hanseni*, *D. gypsophilum*, and *D. variegatum*, quadrivalents are formed by about 70 per cent of the long chromosomes with the submedian centromere, and by about 45 per cent of the long chromosomes with the subterminal centromere. (Likelihood of multivalent formation by the other chromosomes is precluded by their known low chiasma frequency.) Anaphase separation is regular, and the plants are fully fertile. However, it was demonstrated that the chromosomes are not completely homologous, since anaphase bridges indicative of inversions were common.

Of other tetraploids studied, Lawrence (1936) recorded one to four univalents and an undetermined number of multivalents in *Delphinium Ruysii*, a garden hybrid possessing one *D. elatum* (n = 16) and two *D. nudicaule* (n = 8) genomes. A similar condition was found to exist in a group of tetraploid hybrids produced by Mehlquist (unpublished) from crossing *D. elatum* with artificially doubled *D. cardinale*, in which meiotic pairing was found to be primarily by bivalents and univalents, although segregation in succeeding generations indicated that some multivalent pairing occasionally occurred.

Particularly interesting in so far as this study is concerned are the varieties bred by K. Foerster of Bornim, Germany, and studied by Propach (1939, 1940). According to Propach, Foerster produced his hybrids by intercrossing *D. Belladonna* varieties and *D. grandiflorum* var. *chinensis*, obtaining in the first generation fully fertile tetraploids. Later, some of these hybrids were again crossed with *D. grandiflorum* to form sterile triploids (Appendix). Unfortunately, full cytological details were not given. Propach interpreted his results as indicating that there is little genomic differentiation in *Delphinium* and that autopolyploidy is involved.[5]

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[5] However, Foerster (1929) does not give details about the parentage of his varieties in all cases, and of those which he discusses, some he terms *elatum* types and some *elatum* × *grandiflorum* var. *chinense* hybrids. Further, the accompanying plates confirm his statements; therefore a thorough cytological study of these forms is desirable before Propach's conclusions can be accepted.

The first object of this study was to discover whether any morphological differentiation of the chromosomes could be made among species of *Delphinium*, so that, if possible, the component genomes of the polyploid species might be identified. The second phase of the cytological work has dealt with the meiotic behavior of the chromosomes in the species and hybrids. Data obtained from chromosome studies have been supplemented by pollen studies which, to some extent, serve to indicate the degree of fertility of a plant; and pollen measurements have been used, especially of herbarium specimens, to give information (which could not be obtained by other means) on the probable polyploid level of these plants.

METHODS

1. *Somatic Tissues—Chromosomes:*

Although the paraffin method has been the one used by previous workers, it was seldom employed here. This was not only on account of the length of time required to prepare the mounts, but also because root tips from sectioned material did not show the structural features evident in acetic squashes, nor could counts of chromosome number be made so readily. For squash techniques, it was necessary to adapt the method to the particular requirements of the material. Pre-treatment with a spindle inhibitor was found to be essential since the chromosomes of metaphase plates were otherwise obtained in face-view only with the greatest difficulty; further, aceto-carmine did not give the degree of differentiation obtained with aceto-lacmoid. The schedule follows:

a. Actively growing root-tips were removed and treated with a saturated solution of paradichlorobenzene (Meyer, 1945) for 3 to 4 hours.

b. Tips were transferred to 7:3 acetic alcohol (Darlington & La Cour, 1947) for 1 to 5 days. Preparations from material preserved longer than this are not clear enough for studies of details of chromosome morphology, but are adequate for counts.

c. Tips were hydrolyzed in a mixture of approximately 2 drops 0.1 normal HCl and 5–6 drops acetic-lacmoid stain (Darlington & La Cour, 1947), heating on a glass until vapor could be seen, and then letting the tips remain in the mixture for 10 to 20 minutes, or until they became soft. (Sometimes it was necessary to increase the proportion of HCl in the staining mixture in order to soften the tips sufficiently, but generally as little acid as possible was used since an excess decreases staining.)

d. Root tips were rinsed in 45 per cent acetic acid for 5 minutes to about an hour.

e. The deeply stained portion of a tip was transferred to a clean slide, and stain and cover-glass were added. The mount was heated and squashed and then sealed. After the cells were dispersed by gentle tapping, considerable pressure could be applied in order to spread out their contents.

The preparations will keep for about a week if stored in a cool place, but they are best within a few hours after being made.

2. *Somatic Tissues—Nucleoli:*

The Feulgen-fast green squash technique (Darlington & La Cour, 1947) was used. Hydrolysis time was about 20 to 40 minutes.

3. *Meiotic Chromosomes:*

The exact method used depended upon the age and condition of the material. In general, the following schedule was employed:

a. Anthers were killed and fixed in acetic alcohol for several hours to a week or more. (Best results were obtained if mounts were made in about one to four days.)

b. A whole anther was transferred to a slide, flattened with the needle, and stained.

1. Fresh material: acetic lacmoid gave the best results.

2. Older material: a mixture of aceto-lacmoid and aceto-carmine was employed, the relative amount of carmine being increased with increasing age of the material.

3. If the material was not stored for more than two weeks, it could be transferred to 70 per cent ethanol, and thereafter stained with carmine, in which case mordanting was found to be necessary.

c. A cover slip was added and the slide was squashed gently and sealed. After the slide had been sealed it could be heated and again squashed if necessary.

4. *Pollen Studies:*

Preparations were made with either aceto-carmine or acid fuchsin, at least three slides being made for each plant of which the pollen was available. The anthers were taken on different days and from different flowers so that the effect of environmental variation could be observed. A total of 200 pollen grains was counted on each slide, only the deeply staining, normally shaped grains being considered "viable." Where possible, 100 good grains of each individual were measured, but in the triploids the number is understandably considerably less.

Pollen preparations from herbarium specimens were made employing the fast-green glycerine jelly method of Wodehouse (1935).

5. *Illustrations:*

Camera-lucida drawings were made with a Spencer Camera Lucida on a Spencer microscope with 15 × ocular and 95 × N.A. 1.40 apochromatic oil-immersion objective, giving a magnification of 2180 × at table height. Reductions are given with each figure. The photomicrographs were taken with a 1 × Bausch & Lomb fixed bellows camera; magnifications accompany the plates and text-figures.

DETERMINATION OF THE LEVEL OF PLOIDY

While the determination of polyploid level in the living plants was always made by chromosome counts from root-tip preparations, the impossibility of applying direct methods to plants represented only by herbarium material made necessary the use of the indirect method of pollen measurement. In studying the percentage of "viable" pollen produced by hybrid individuals, it had previously

been noted that diameter of the pollen grain was a good indicator of the polyploid level of the plant (Table I). For the plants measured there was good separation of diploids and tetraploids on this basis. The hexaploids and triploids generally produced the largest pollen, although there was some overlapping between these and *D. elatum*. It is to be noted that pollen production by the triploids is very low (except in the colchicine-treated spike of 50-40-2, which is presumed to have been doubled); the similarity in size of their few pollen grains to that of the hexaploids is an indication that the pollen from these plants is unreduced, and hence triploid.

For pollen grains of the herbarium specimens, size of pollen grain was again found to be a differential character for the polyploid level, although the actual sizes obtained were somewhat smaller in all classes, as might be expected on the basis of the difference in the suspending medium of the stain and from long drying of the material (Table II).

CYTOLOGY OF NATURAL SPECIES, *DELPHINIUM BELLADONNA*, AND THE TRIPLOIDS

Morphology of the Somatic Chromosomes.—

In view of the general similarities in size of the chromosomes already noted as characteristic of the genus, ideograms are presented here for two species only: *D. grandiflorum* var. *chinensis* and *D. cheilanthum*. The *A* and *B* chromosomes of these species probably are to be compared with similarly lettered chromosomes in the ideograms of Lewitsky (1931) and Lewis *et al* (1951), but because of the similar sizes of the smaller chromosomes it is not to be assumed that these are comparable to similarly lettered chromosomes in the other ideograms.

The major distinguishing features of the genomes figured here (pl. 13) have been the satellite-bearing chromosomes. The presence of nucleolar-organizing satellited chromosomes in the complement of many plants has been often noted since the classic papers of Heitz (1931), Navashin (1934), and McClintock (1934). Later, the discovery of polyploid species in which the satellite number was comparably increased led certain workers to assume that often, if not always, apparently diploid species which possessed several satellites in the gametic complements are actually of polyploid derivation. This was the view held by Gates, who published a comprehensive review on this subject in 1942. However, since many polyploids never have more than two satellites, and since, on the other hand, in such plants as *Leontodon leysseri* three of the four chromosomes of the haploid complement bear satellites (Elliot, 1950), inferences as to polyploid level based on satellite or nucleolar number alone must be regarded as unsound.

Another problem related to the existence of satellites must be considered in order to appreciate the variations in satellite number observed in the *Delphinium* hybrids, and that is differential amphiplasty. This phenomenon was first noted by Navashin (1927, quoted by him in 1934), who applied the term to the apparent loss of satellites which sometimes occurs in hybrids. The following year, McClintock, in her paper on the nucleolar organizing chromosome of *Zea Mays*,

discussed in detail Navashin's work, interpreting the loss of satellites in hybrid forms as being due to the inability of the chromosome to "organize" a nucleolus in the presence of another more "active" chromosome. Amphiplasty has recently been reported in the genus *Leontodon* (Elliot, 1950), and had been occasionally reported in other genera (Meurman and Therman, 1939; Levan, 1937).

While our present understanding of differential amphiplasty is by no means perfect, the cases cited above seem to show that under certain conditions such as obtain in some hybrid cells, the apparent morphology of nucleolar organizing chromosomes may be modified. Since the presence of a satellite at metaphase is usually directly related to the formation of a nucleolus in that region in the preceding telophase, then the causative factor is apparently related to nucleolar metabolism. Nevertheless, the actual physiological differences between individual nucleolar "organizers," which are the essence of the problem, are not known at all, and it is therefore the morphological aspect of the phenomenon which concerns us here.

Diploids.—In pl. 13 is given the ideogram of *D. grandiflorum* L. var. *chinensis* Fisch. hort. var. Blue Butterfly, pollen parent of the 48-27 and 48-6 series of triploids. The actual length of metaphase chromosomes ranges from 3.1 to 10.1 μ. (These measurements are based on chromosomes not artificially contracted by PDB, although the chromosomes measured were subjected to minimum treatment in order that the spindle would not interfere with their being well-flattened.) Of the shorter, subterminally constricted chromosomes, chromosome *H* is readily identified by its length as well as by the satellite; of the rest, chromosome *C* may be identified by its satellite and sometimes by the secondary constriction of the long arm. Chromosomes *D* through *G* are individually distinguishable only with difficulty; the lengths of their short arms, on the whole, were found to be more diagnostic than the long arms, which may be variously extended, being slower to complete their coiling cycle than the short arms.

A difference in the activity of the satellites was noted here. While usually both *C*'s were satellited, no cells were ever observed in which at least one *C* did not bear a satellite; the satellite of the *H* chromosome, on the other hand, was commonly present in unicate, and sometimes was even missing altogether. This was generally true for all plants of *D. grandiflorum* and was statistically determined for two individuals (Table III).[6]

Related plants, including 47031-1 from the Royal Botanic Gardens at Kew, *D. grandiflorum* L. var. *chinense* Fisch. from Basel, and numerous plants of horticultural varieties such as Tom Thumb and White Butterfly were examined and found to have a similarly differentiated complement (pl. 13). 47031-1 was found to possess a telocentric fragment, about the length of the long arm of the *H*

[6] In the course of numerous observations, in one plant of this species a third satellite was noted on one of the intermediate chromosomes, but as it was not present in any other case it has been omitted from the ideogram.

chromosome. Though the numbers of fragments present in different cells of an individual have been found to vary somewhat, the fragment is commonly transmitted through the gametes, being found in plants three and four generations removed from 47031-1. Unfortunately, the original plant and the fragment-bearing triploids were lost before pairing affinities of the fragment could be determined, and there are sufficient irregularities in the descendant hexaploids to make its identification in PMC's doubtful.

Plants of *D. tatsienense* Franch., a species closely related to *D. grandiflorum* L., were found to possess a genome similarly differentiated except that in the individuals surveyed the satellite is as often developed on the *H* chromosome as on the *C* chromosome (see 51-311-9, Table III).

D. cheilanthum.—By contrast with *D. grandiflorum*, *D. cheilanthum* bears its satellites on the *A* and *C* chromosomes, that on the *A* being not only larger but also the more "active" of the two (Table III, 51-307-6 and 51-307-1). So far as can be ascertained, the chromosomes of the two species are otherwise similar, except that the satellite-bearing arm of *A* is slightly longer here than in *D. grandiflorum*.

TABLE III

SATELLITE EXPRESSION IN *DELPHINIUM* SPECIES AND HYBRIDS

Plant	Fraction of chromosomes bearing satellite*			Number of cells	Theoretical satellite number	Actual average satellite number
	C	H	A			
Diploids						
grandiflorum						
51-312-6	0.94	0.48	—	100	2:2:0	1.8:1.0:0
51-315-6	0.91	0.62	—	100	2:2:0	1.8:1.2:0
tatsienense						
51-311-9	0.85	0.80	—	100	2:2:0	1.7:1.6:0
cheilanthum						
51-307-6	0.47	—	0.95	100	2:0:2	1.0:0:1.9
51-307-1	0.49	—	0.98	100	2:0:2	1.0:0:1.9
Tetraploids						
D. elatum						
51-318-2	0.56	0.12	0.83	21	4:2:2	2.2:0.25:1.6
51-318-4	0.50	0.07	0.92	71	4:2:2	2.0:0.15:1.8
Triploids						
48-27-3	0.61	0.33	0.05	100	3:2:1	1.8:0.67:0.05
50-15-3	0.52	0.34	0.63	100	3:2:1	1.5:0.68:0.63
Hexaploids						
Smith's *Belladonna*	0.63	0.10	0.84	25	6:4:2	3.6:0.4:1.6
51-232-4	0.45	0.25	0.13	60	6:4:2	2.7:1.0:0.3

* Fraction is computed on the basis of the actual observed maximum number of satellites for that chromosome.

Other diploids.—A third situation with respect to satellite number and position was found in *D. cardinale* (pl. 13) and *D. nudicaule* from California, and a fourth in *D. Zalil* Aitch. and Hemsl. (native to Persia and Turkestan) and *D. sulphureum* Boiss. and Hausskn. (from north Syria). In the California species the satellite number is 3, and the satellites occur on the *H* and on two pairs of intermediate chromosomes, one of which may or may not correspond to *C*, the lengths of the chromosomes in these species being not exactly comparable to those of *D. cheilanthum* and *D. grandiflorum*. The third satellite is on the second shortest chromosome. Despite the high potential satellite number, the low number of nucleoli usually present at telophase and interphase (generally no more than 4) indicates that all are rarely active in a particular mitotic cycle. In *D. Zalil* and *D. sulphureum* satellites occur on *A* and on one of the intermediate chromosomes. However, the genome differs from that of *D. cheilanthum* in the arm lengths of the intermediate chromosomes, so that direct comparisons cannot be made.

In studying satellite development in the above diploid species a situation was noted which has apparently not been described before, namely, that even within old diploid species differential "activity" of satellited chromosomes may be common. With this in mind further variations in satellite development which are found in polyploid species may not be so unexpected. In order to avoid ambiguity here, I shall use the term "differential activity" to apply to the differences in satellite development such as characterize diploid species, and "amphiplasty" to refer to any pronounced alteration in differential activity which follows hybridization. Actually, however, it is not to be assumed on such scanty visual evidence that any physiological distinction is being made.

Tetraploids: D. elatum.—In *D. elatum,* the only tetraploid species observed, distinctions among the chromosomes are again difficult to make. There are 2 pairs of long, medianly constricted *A* chromosomes, 2 pairs of long, sub-medianly constricted *B* chromosomes, 10 pairs of intermediate chromosomes with subterminal constrictions, and two pairs of short chromosomes with subterminal constrictions. Amphiplasty obscures the satellite situation, the more active *A* and *D* satellites usually being the only ones present (Table III), but a study of a large number of cells, both in the species (accessions from Göteborg Botanic Garden, and the Royal Botanic Gardens at Kew) and of horticultural variants, indicates the presence of satellites on 1 *A*, 2 *C*'s and 1 *H* of the haploid complement. Although the number of satellites in the tetraploids parental to the triploids could not be determined statistically, camera-lucida drawings of the complements of 47-98-3 and Summer Skies indicate that these plants were typical in this respect (pl. 14). As in *D. cheilanthum*, the satellited *A* chromosome stands out from its counterpart in the other genome by virtue of its longer satellited arm. Lewitsky (1931) noted this difference in length, but did not observe the satellite.

The nature of the chromosome differentiation in *D. elatum* is thus strongly suggestive of an allopolyploid origin by hybridization and subsequent doubling of the chromosome number of diploid forms whose chromosome complements were of

the types represented in present-day species *D. grandiflorum* and *D. cheilanthum*. That the chromosomes designated at *C* are truly comparable in the two genomes and are not different members of the medium-sized group is corroborated by the fact that both possess a secondary constriction of the longer arm.

Aneuploids are occasionally found, even among the plants from the botanic gardens. However, they do not possess the abnormal characteristics which ordinarily distinguish aneuploids on the diploid level, and fertility, as judged by amount of seed produced, is apparently not greatly impaired.

Triploids.—All plants of the four groups of triploid hybrids were examined and found to be essentially similar in so far as the morphology of the chromosomes is concerned (pl. 14). The maximum satellite number in each is 6: 1 *A*, 3 *C*'s, and 2 *H*'s, as would be expected on the basis of the generally regular segregation of the parents. The precise situation as to satellite development has been thoroughly worked out only for two individuals, 48-27-3 and 50-15-3, most of the other plants having died before this part of the study was undertaken. An interesting case is 48-27-3, in which the satellited *A* chromosome, so active in *D. elatum*, is rarely developed. (Study of camera-lucida drawings of other plants of this line and of the very similar 48-6 line indicates that this is generally true of both groups.) However, in 50-15-3, the other triploid analyzed, the *A* satellite was observed in more than 80 per cent of the cells examined. Thus, in crosses of similar parentage, amphiplasty has been demonstrated in one case, but did not occur in another.

With regard to the centric fragment of their pollen parent 47031-1, triploids 50-15-1 and 50-15-4 were found to possess the fragment in most cells; 50-15-3, 50-40-1, and 50-40-2 lack the fragment.

Hexaploids.—The tendency already noted for partial suppression of the potential satellite number was especially evident in the hexaploids, of which Smith's *Belladonna*,[7] Cliveden Beauty, Bellamosum, and Lamartine were observed in some detail, as well as in the derived hexaploids which are to be considered in chap. V. In most cases, cumulative records on these plants indicated a possible satellite number of 2 *A*'s, 6 *C*'s, and 4 *H*'s of the diploid complement. However, the normal satellite number in individual cells is often only half this number (pl. 15).

When interplant variation in degree and type of amphiplasty was studied Smith's *Belladonna* was found to possess very active *A* SATs, but among its progeny obtained by selfing, all degrees of activity were found; this was also true of the F_1 obtained by crossing this plant with Bellamosum. At the other extreme are certain individuals of Bellamosum, in which the satellited *A* can rarely be distinguished (Table III).

Meiosis and Fertility.—

Meiotic studies have been made of the triploid hybrids and their parents, where these have been available, as well as of *Belladonna* varieties, in an effort to compare

[7] The plant termed "Smith's *Belladonna*" throughout this study is a selection from the horticultural variety "Cliveden Beauty."

TABLE IV. MEIOSIS OF THE TETRAPLOIDS

Plant	Metaphase configurations							First Anaphase				Second Anaphase			
	16 II	15 II, 2 I	14 II, 4 I	13 II, 6 I	12 II, 8 I	11 II, 10 I	Number of cells	Number cells structurally abnormal	Number cells structurally normal	Total	% abnormal	Number cells structurally abnormal	Number cells structurally normal	Total	% abnormal
47-98-3	18	2	0	0	0	0	20	88	112	200	44.0	4	16	20	20.0
Summer Skies	11	7	5	0	0	1	24	11	124	135	11.3	3	31	35	10.3

TABLE V. METAPHASE PAIRING IN THE TRIPLOIDS

Plant	8 II, 8 I	7 II, 10 I	6 II, 12 I	5 II, 14 I	4 II, 16 I	3 II, 18 I	2 II, 20 I	1 II, 22 I	24 I	1 III, 7 II, 7 I	1 III, 6 II, 9 I	1 III, 5 II, 11 I	1 III, 4 II, 13 I	1 III, 3 II, 15 I	1 III, 2 II, 17 I	1 III, 1 II, 19 I	1 III, 21 I	Total cells
48-27-2		2	7	7	5	2	6	2			2	1	2	1				37
48-27-3	20	14	9	9	8	2	1			3	4	2	2					74
48-27-5	20	18	20	18	6	1				3	2	1	1					92
48-27-6	2	3	5	7	1	5	1				1	1	4					30
48-27-12		1	3	5	6	2	2	2				3	1					25
48-6-1		2				1	1			1								5
8-6-3			1	1	3	1												6
50-15-1	1			6	2	5							2	2	1			19
50-15-3	30	7	7	1	2													47
50-15-4		3	3	1	3	3	1	1										15

chromosome homologies in the triploids and *Belladonna.* Early prophases are usually difficult to stain by squash methods, and while fair preparations can be made by paraffin sections, using gentian violet stain, the high number of chromosomes present makes prophases generally of less use than later stages, which can readily be stained by conventional squash methods. For the most part, configurations at diakinesis and metaphase were analyzed, and anaphase I and II were scored for structural abnormalities. However, counts of chromosome segregation were not made, since the frequent occurrence of aneuploids in all polyploid populations is sufficient evidence that hyperploid and hypoploid gametes are produced.

The approximate percentage of "viable" pollen produced by certain key plants is given in Table I. However, since samples from the same plant taken on different days may show a wide range of viability, the values given can scarcely be considered absolute indications of fertility. Moreover, apparently good grains may not survive until the pollen tube has reached the ovule, not only on account of some deficiency of the grain, but also, perhaps, because of incompatibility with the stylar tissue. Certainly, the particular environmental conditions prevailing at the time of pollen formation and shedding are not the least important factor in the production of functional pollen and its further development. It has repeatedly happened that a plant which produced a large amount of well-filled, staining pollen grains and set a high percentage of viable seeds at one time, produced little pollen and set few seeds at another time, or again, produced apparently good pollen but set no seed. The immediate cause of impaired fertility of this sort is often a prolonged hot spell, but other factors may have a similar effect.

Diploids.—Blue Butterfly is usually quite regular in meiosis. In almost every one of numerous cells examined at diakinesis and MI, pairing was in 8 bivalents (pl. 15). Chiasma frequencies ranged from 2 to 3 for chromosomes *A* and *B*, to 1 or occasionally 2 for the others. Anaphase separation is quite regular, bridges occurring in less than 1.0 per cent of the cells examined. A regular second division is followed by the simultaneous cleavage of the pollen mother cell into tetrads.

Unfortunately, metaphase pairing of 47031-1 was not observed during the first year and the plant was subsequently lost. In anaphase I, however, laggards (probably the fragment) were noted in 9 per cent of the cells, and bridges in 3 per cent of the cells. The amount of "viable" pollen was about 65 per cent. The presence of the fragment in two of the five triploid offspring of this plant is satisfactory indication that pollen fertility was not prevented by the possession of the fragment. However, whether the failure of the plant to set any seed when self- or cross-pollinated may indicate some deleterious effect of the fragment in the ovule cannot now be shown. This case thus appears to be quite different from that of the centric fragment studied by Rhoades in *Zea* (1940), where transmission of the fragment was largely through the egg, fragment-bearing pollen grains usually not competing successfully with normal pollen grains.

Tetraploids.—Meiosis of Summer Skies is not entirely regular, the occurrence of 2 to 4 univalents at metaphase I being rather frequent. Further evidence of

structural hybridity is given by anaphase I and second-division configurations, bridges, fragments, and lagging chromosomes being present in 11.3 per cent of the A I and 23.3 per cent of the A II cells examined (Table IV). Pollen viability appeared to be rather low (Table I), but that the plant is highly fertile has been indicated by the amount of seed produced.

47-98-3 exhibited fairly regular pairing; only two of the twenty diakinesis and MI plates showed each 2 univalents. However, a higher proportion of the large chromosomes had reduced chiasma frequency, with sometimes only 1 chiasma per bivalent. Further evidence of chromosomal hybridity is seen in the rather high number of cells at anaphase I which showed visible abnormalities (44.0 per cent). Abnormalities of the second division were less frequent, being present in only four of twenty cells examined. Pollen viability was about 65 per cent.

47-2-3, the tetraploid parent of the 48-6 group, was not available for study.

Triploids.—Representatives of the several crosses have been analyzed. Since the number of PMC's examined in each case have not been large enough to permit separate discussion, the data have been somewhat grouped.

48-27-: Numbers 2, 3, 5, 6, and 12 have been studied (Tables V and VI, pl. 15). Metaphase pairing is largely in bivalents and univalents, only 34 trivalents having been found in the 258 cells analyzed. Usually, the long chromosomes (*A* and *B*) were involved in the trivalent configurations, but trivalents formed by chromosomes of intermediate size were found at least twice. The low number of trivalents involving the intermediate chromosomes may be due in part to their observed low-chiasma frequency, but also to the presence of differentiated segments. The amount of even the *A* and *B* chromosomes present in trivalents is only 7.2 per cent.

In two individuals (48-27-3 and 48-27-5) bivalent formation is near the maximum number expected if normal chiasma frequencies prevail—that is, if those chromosomes which pair form the normal number of chiasmata. However, whether such pairing is ordinarily between the 8 chromosomes contributed by *D. grandiflorum* and 8 chromosomes of *D. elatum*, or whether pairing is primarily within the *elatum* complement only can not be determined precisely. The above-mentioned occurrence of occasional trivalents does indicate that some mixture of the two sorts prevails. That intragenomic pairing may occur in *D. elatum* is already known from the work of Lawrence (1936) and Mehlquist (unpublished); but the morphological similarity of one *D. elatum* genome to that of *D. grandiflorum* is equally strong indication that pairing between these chromosomes cannot be discounted.

Despite the rather high proportion of bivalents which may be formed in certain individuals, the frequency of univalents, which may sometimes number as many as 22, is indicative of structural differentiation of the chromosomes. This is further substantiated by the high percentage of structural abnormalities observed at anaphases I and II. At least one bridge-fragment was observed, on the average, in about 50 per cent of the cells examined, both at A I and at A II. Such config-

TABLE VI
MEIOTIC ANAPHASES OF THE TRIPLOIDS

Plant	Anaphase I						Anaphase II					
	Bridges & fragments	Laggards	Both	Structurally normal	Total	Per cent abnormal	Bridges & fragments	Laggards	Both	Structurally normal	Total	Per cent abnormal
48-27-2	16	17	10	21	64	67.2	7	1	5	17	30	43.3
48-27-3	41	61	14	92	208	55.8	16	15	11	25	67	62.7
48-27-5	29	33	12	33	107	69.2	12	7	5	35	59	40.7
48-27-6	10	21	9	23	63	63.0	—	—	—	—	—	—
48-27-12	44	25	16	39	124	68.4	—	—	—	—	—	—
48-6-1	36	10	7	29	82	64.7	3	1	3	7	14	50.0
48-6-3	13	10	6	25	54	53.7	13	11	5	10	39	74.3
50-15-1	21	8	4	34	67	50.9	10	6	7	7	30	76.6
50-15-3	14	1	4	28	47	40.5	11	4	4	22	41	46.3
50-15-4	19	2	4	37	62	40.3	—	—	—	—	—	—

urations have been shown by others to be caused by crossing-over within inversions, by crossing-over involving certain types of duplication (McClintock, 1941) or, as suggested by Emsweller and Jones (1938), by pairing between chromosomes whose insertions are not opposite.

The number and behavior of the lagging chromosomes are of interest. The average number of laggards was less than one per cell in A I, and even lower in A II. As a result, except for the numerical imbalance of most of the gametes formed by these plants in natural consequence of their triploid constitution, the loss of univalent chromosomes, which is often characteristic of such plants, was not pronounced. This point will be considered further in the treatment of the hexaploids.

The number of microspores per tetrad is variable, 2 and 3 being the more common variants, but a fifth micrograin is occasionally formed. Micronuclei are extremely common, but are usually included with one of the other nuclei within a common wall.

The amount of apparently good pollen has been found to be quite small, and that which is formed is within the range of pollen size of the hexaploids, suggesting that such pollen is actually unreduced (Table I).

48-6-: Numbers 1 and 3 of this line were briefly analyzed. There was apparently a greater tendency to bivalent formation in 48-6-1, 7 II having been noted in several cases, while 2–6 II were found in 48-6-3. One trivalent was noted in 48-6-1. In anaphase I and anaphase II somewhat higher frequencies of abnormalities were noted in 48-6-1 than in 48-6-3.

Viable (unreduced) pollen grains were formed in 2.8 per cent of cases in 48-6-3 and 5.7 per cent in 48-6-1 (pl. 15).

50-15-: Numbers 1 and 4 have been examined and seem to differ somewhat in pairing relationships. Single trivalents involving the large chromosomes occurred in 5 of 18 figures in 50-15-1, whereas no trivalents were noted in the 15 cells of 50-15-4 analyzed. Structural abnormalities at A I were present in about 40 per cent of the cells of each, and there were many irregularities at A II. Pollen viability was determined at 1.5 per cent and 2.5 per cent for numbers 1 and 4 respectively.

50-40-: A survey of meiosis in 50-40-2 indicated that pairing was usually in 5 to 7 bivalents, with an occasional trivalent. Reduced chiasma frequency was evident in the *A* and *B* chromosomes, and abnormalities of later stages were frequent.

Moerheimi was lost early in the study, but preliminary observations indicated that meiosis was comparable to the three hybrid groups. Pollen viability was extremely low, less than 0.5 per cent unreduced pollen grains having been found.

Hexaploids.—Belladonna: Lawrence (1936) has reported that meiosis in this form is largely regular. In Cliveden Beauty, a light-blue *Belladonna* variety, 2 to 4 univalents (of small or intermediate chromosomes) were noted in 10 out of 16 MI cells, but the chiasma frequency of the *A* and *B* chromosomes was only slightly reduced. At anaphase I structural abnormalities were visible in 12.3 per cent of the cells. Anaphase II was quite regular, only 7 of 121 PMC's being visibly abnormal. Individuals of this variety were found to have from 63.2 to 80.5 per cent of good pollen.

Preparations of Smith's *Belladonna* showed somewhat less regular pairing at metaphase, with up to 8 univalents and the *A* and *B* chromosomes often with but one chiasma per pair. The actual amount of pairing was somewhat higher, however, for in diakinesis univalents were uncommon and the large chromosomes had mostly two or three chiasmata in each bivalent (Table VII, pl. 15).

Table VII gives some indication of the irregularities which are found in *D. Belladonna* varieties, although the plants cited by no means represent a random sample. A certain number of univalents are almost always present, but they assort at random and do not commonly lag at the plate. Multivalents are rare, but were noted in 52-325-11 (Smith's *Belladonna* × self), where both the *A* chromosomes and intermediate chromosomes were observed in such configurations. However, although one *A* chromosome was lacking from this plant, the monosome was unusually unpaired.

The consequences of such irregularities as have been observed in *Belladonna* are indicated by somatic counts in various populations involving this variety. Text-fig. 7 compares the range in chromosome numbers of randomly selected progeny of various crosses. Thus, in 51-224 (Smith's *Belladonna* × Bellamosum, a dark blue *Belladonna* segregate) 8 of the 15 plants in the sample possessed 48 chromosomes, and in 52-311, produced by selfing a 48-chromosome individual of

TABLE VII
MEIOSIS IN BELLADONNA TYPES

Plant	Metaphase I						Anaphase I				Anaphase II			
	Chromosome number	Number of cells	Number bivalents per cell—range	Total number multivalents	Number multi. involving intermediate c-somes	Median number bivalents	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells
Smith's Belladonna*	48	55	24–20	0	0	23	12	2	2	33.3	Mostly regular			
Cliveden Beauty-5	48	15	24–22	0	0	23	81	3	3	7.4	121	4	3	5.8
52-325-11	47 (5A)	32	23–19	4	2	22	48	3	9	25.0	—	—	—	—
51-224-16	48	21	24–22	0	0	23	29	4	7	35.9	14	1	0	0.7
51-232-47	49	45	24–19	0	0	23	100	9	34	43.0	65	4	19	35.4
Lamartine	48	46	24–21	0	0	23	67	6	4	14.9	104	7	6	12.5

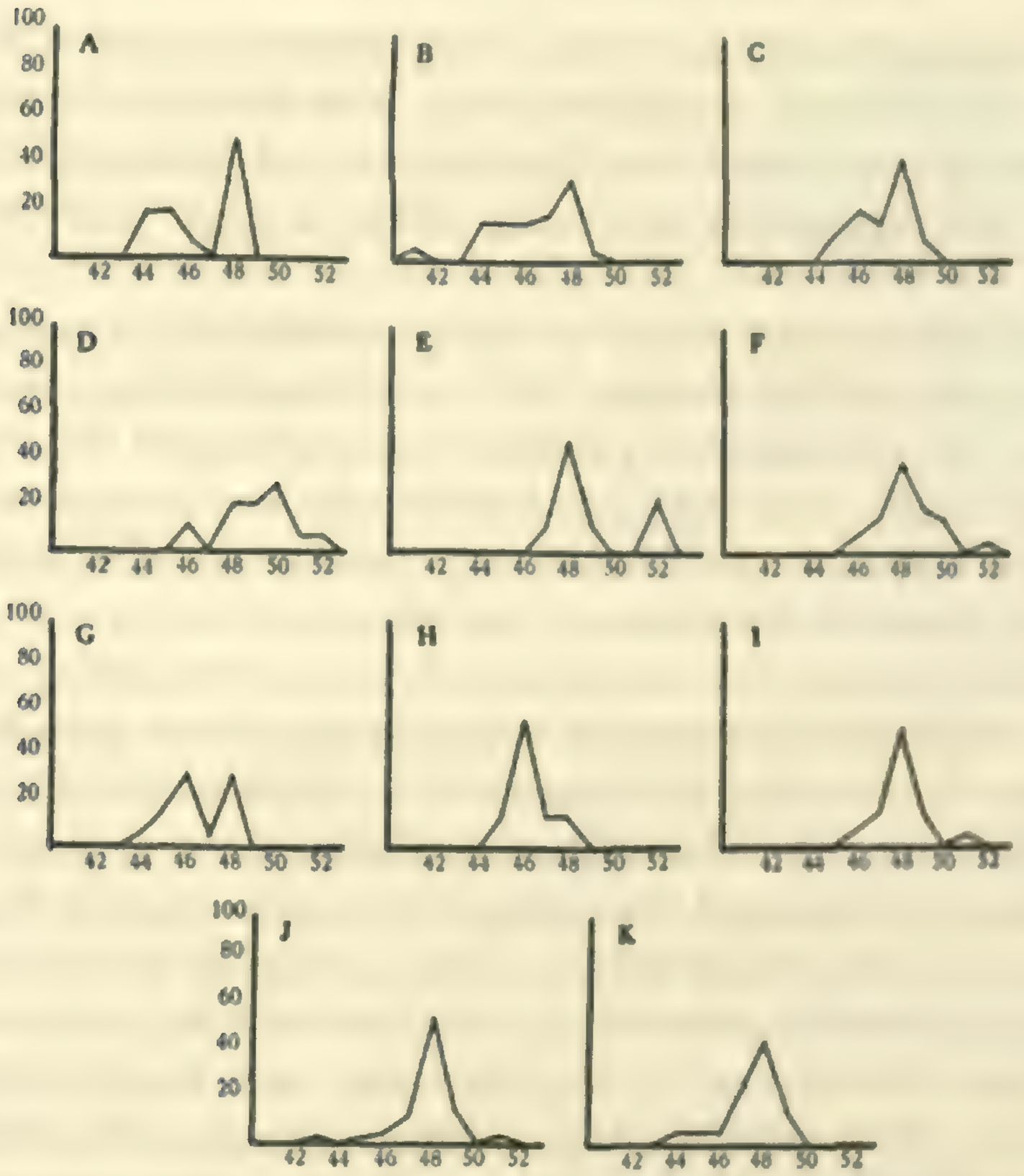
*Of 21 late prophases observed. 17 showed 24 II, and 3 had each 23 II and 2 I. One cell had 6 univalents.

this population, chromosome numbers of 25 plants ranged from 41 to 49, only 7 individuals having the "normal" number. Again, among 25 individuals of cross 51-232 (Bellamosum × self) chromosome numbers ranged from 45 to 49, 11 plants having the 48 chromosomes expected. In a sample of 10 plants obtained by selfing Smith's *Belladonna* (not figured), numbers ranged from 46 to 48. In most of the above cases the additional or missing chromosomes were of the smaller classes, but one plant with 48 chromosomes (51-232-1) lacked an *A;* and 51-224-13, with 45 chromosomes, lacked a *B.* None of the aneuploids were visibly abnormal, and such observations of pollen viability as were made revealed no obvious correlation between chromosome number and pollen viability. Evidently, like many other polyploids, *D. Belladonna* can withstand the loss of a certain amount of genetic material without suffering the consequent weaknesses and abnormal development common when such losses occur at the diploid level.

Discussion and Summary.—

The cytological information given above bears on the problem of the identity of the genomes in *D. Belladonna* both from the standpoint of chromosomal morphology and of pairing homologies of the chromosomes in meiosis.

The somatic studies have made clear that the aspect of the chromosomal complement of *D. Belladonna* is just what might be expected if it had been produced by doubling the chromosome number of such a triploid as those produced here. The amphiplasty of the satellite of the *A* chromosome in different plants of *Belladonna* was also found in different triploids. That this differential activity is



Text-fig. 7. Frequency distributions of chromosome numbers in populations of *D. Belladonna* and of the derived hexaploids. Ordinates represent per cent of population; abscissa, number of chromosomes.

A—51-224	D—51-216	G—51-219	J—51-222
B—52-311	E—51-217	H—51-220	K—51-223
C—51-232	F—51-218	I—51-221	

not equivalent to morphological loss of the satellite was made evident by analyses of certain plants in which the rare occurrence of the satellite proved that its usual absence does not represent permanent loss. This condition is thus different from the actual morphological differences in satellite disposition between the chromosomes of the two diploids *D. grandiflorum* and *D. cheilanthum*.

Recognition of this difference is important for the interpretation of the satellite pattern in *D. elatum*, the various triploids, and *D. Belladonna*. Thus, *D. elatum* might be a derivative of two diploid species whose genomes were differentiated along the lines of present-day *D. grandiflorum* and *D. cheilanthum*. And, given *D. elatum* as the tetraploid parent of *D. Belladonna*, *D. grandiflorum* might be the diploid parent; but *D. cheilanthum* could not have been, unless drastic morphological alterations of the chromosomes have ensued since the time of origin of *Belladonna*. If the alternative supposition is made, that *D. cheilanthum* was the diploid parent of *Belladonna*, again, as with the morphological characters, there is the problem of finding a tetraploid other than *D. elatum* in the gardens of Europe—a tetraploid, moreover, both of whose genomes of the haploid complement are similarly differentiated.

Analysis of pairing homologies of the chromosomes has proved illuminating in some respects, though not so useful in others. This was not unexpected, since in polyploids above the tetraploid level all combinations of autopolyploidy, segmental allopolyploidy, and amphiploidy may exist within a single individual (Stebbins, 1947, 1950).

The triploid hybrids were found to exhibit neither the complete absence of pairing characteristic of the progeny of crosses between very distantly related species, nor the relatively complete pairing of some segmental allopolyploids, or of autopolyploids. True, as has been pointed out, the low metaphase chiasma frequency of the chromosomes would ordinarily prevent trivalent formation by all except the large *A* and *B* chromosomes, but the actual number of univalents was ordinarily higher than the eight expected if heterogenetic pairing either between *grandiflorum* and *elatum* chromosomes or within the *elatum* complement were of regular occurrence. Actually, the formation of occasional trivalents by the large chromosomes indicates that such pairing as does occur is a mixture of the two sorts.

It has repeatedly been noted that pairing of chromosomes in the F_1 of such a species cross cannot be taken to indicate that a polyploid derivative of the cross (here a hexaploid) would necessarily be characterized by corresponding multivalent formation (Darlington, 1937; Goodspeed and Bradley, 1942; Clausen, Keck and Hiesey, 1945; Stebbins, 1947, 1950). Rather, after doubling has occurred, differential affinity of the chromosomes may result in regular bivalent formation, not only in allopolyploids (Clausen and Goodspeed, 1925; Buxton and Newton, 1928; Kagawa and Nakajima, 1933) but even in known autopolyploids (Skirm, 1942).

Since each case must be considered individually and the direct hexaploid derivative has in this instance not been produced, the triploids can best be described as being the sort of plants which might well give rise to segmental allopolyploids, the low chiasma frequency of whose chromosomes would, on the whole, lead to more-or-less regular bivalent formation in the hybrid. One should expect, then, relatively little segregation in future generations, and the plants would continue to possess the more-or-less intermediate appearance of the triploids.

The cytology of *Delphinium Belladonna* itself suggests that this species behaves rather like a segmental allopolyploid, but with perhaps fewer aberrations than are generally found in polyploids of this type. Thus, while at first metaphase, pairing is primarily by bivalents, still the formation of univalents is not uncommon. Multivalents are rarely found.

A consequence of univalent formation in gametogenesis is the production of numerous aneuploids. The mere occurrence at the polyploid level of viable aneuploids of good fertility is not unknown (Sears, 1944; Clausen and Cameron, 1944), although their high frequency here was not anticipated. In *Triticum aestivum* and *Nicotiana tabacum*, most of the nomosomics and nullisomics are individually recognizable, and this has been found to be true in certain other polyploid hybrids where aneuploids have been found (*Primula kewensis*, Newton and

Pellew, 1929; *Nicotiana tabacum*, Clausen and Goodspeed, 1924; *Nicotiana rustica*, Lammerts, 1932; *Nicotiana glauca* × *N. Langsdorffii*, Kostoff, 1939). However, while a part of the variability within *Belladonna* may be owing to aneuploidy, still it has not been possible to isolate any characteristic monosomic phenotypes, even for the large chromosomes, suggesting that there must be a considerable amount of duplicated chromosomal and genetic material in *D. Belladonna*.

This conclusion is corroborated by a survey of the extent of hypoploidy which *Belladonna* tolerates. Plants having from 43 to 44 chromosomes, while apparently infertile, are not themselves weaker than their euploid sibs. In most allopolyploids with fully differentiated genomes, such aneuploids as occur are usually deficient for no more than one or two chromosomes (Newton and Pellew, 1929; Müntzing, 1937). It is in plants in which the genomes contain many homologous chromosomes or chromosomal segments that extreme aneuploids have generally been found (Müntzing, 1937; Myers and Hill, 1940; Myers, 1947; Love and Sunneson, 1945).

Since the univalent chromosomes are usually included in the daughter nuclei, the prevalence of hypoploids among the plants of all the *Belladonna* populations studied can be explained on the assumption that in these relatively balanced plants, a gamete deficient for one or several chromosomes is at an advantage over gametes containing chromosomes in excess. Therefore, those gametes which function would then include 24 or fewer chromosomes. It is not, however, to be concluded that *Belladonna* is insensitive to chromosome losses of indefinite extent: on the whole, aneuploids with 46 or 47 chromosomes are the most frequent, so that functional gametes must not, as a rule, lack more than one or two chromosomes. Further, though intervarietal crosses are easily made, the germinability of seeds produced is higher in selfs than in intervarietal crosses (Table XI). It seems, therefore, that such chromosomal differentiation as exists between varieties may result in sufficient deficiencies either in the embryo or in the endosperm that in consequence the hybrid seed is less viable. Finally, since fertility tends to be generally higher in the more nearly euploid individuals, and the progeny of the aneuploids do not vary more in chromosome number than do the progeny of normal individuals, *D. Belladonna* Hort. maintains itself approximately at the hexaploid level.

Of the many allopolyploids which have been analyzed (Stebbins, 1947, 1950) the one perhaps most similar to *D. Belladonna* is the segmental allopolyploid *Anemone Jancewskii* (= *A. sylvestris* × *A. multifida* var. *magellanica*), first synthesized by Jancewski before 1892, resynthesized by Gajewski (1946), and further, occasionally spontaneous in botanic gardens. Morphologically, the hybrid is intermediate between the parents and is quite constant, even aneuploids not being of abnormal appearance. A cytological study of the parents and the hybrids by Gajewski revealed that in the triploid (24 chromosomes) at MI from 3 to 8 bivalents are formed, the remaining chromosomes being unpaired. In the F_2 generation produced by the functioning of unreduced gametes (Jancewski reported two instances of somatic doubling but Gajewski did not obtain any hexa-

ploids by this means), in addition to cells in which 24 bivalents occur, in other cells there were some univalents and from 1 to 3 multivalents. Seed and pollen fertility in different individuals of this generation ranged from rather high to rather low, and in the F_3 there was a general increase in fertility. The chromosome numbers were uniformly about 48 in Gajewski's plants, but in the accessions from botanic gardens they ranged from 42 to 48. The chief respect in which *A. Jancewskii* seems to differ from *D. Belladonna* and from the hybrids synthesized here is in the complete absence of trivalents in the triploid and in the higher frequency of multivalents in the hexaploid. The first may be due to greater differentiation of the parental genomes; the second may well be the result of the much higher chiasma frequency of the chromosomes of this hybrid.

To summarize, then, although *D. Belladonna* has previously been considered an amphidiploid on the basis of its largely regular meiosis and its relatively constant appearance, intermediate between certain diploid and tetraploid species of cultivation, the garden hexaploid has been shown to have somewhat less regular meiosis than is characteristic of true amphidiploids. This is indicated both by the common occurrence of univalents and other irregularities in meiosis, and in the higher production of viable, fertile aneuploids than is characteristic of such plants. Rather, *D. Belladonna* may better be classed as a segmental allopolyploid, in which the low chiasma frequencies of the chromosomes tend to enforce bivalent formation, and morphological constancy is further enhanced by the quantitative mode of inheritance of many of the differentiating characters.

DERIVED HEXAPLOIDS

For descriptive purposes, all of those plants having in their ancestry one of the triploids and *Belladonna* have been termed "derived hexaploids." The pedigrees of the major lines are given in text-fig. 2.

First-generation Hybrids: Triploids × *Belladonna Varieties.*—

The dangers of making decisions regarding the nature of polyploidy in a hybrid, whether it be a segmental allopolyploid or an amphiploid, have been pointed out by Stebbins (1947, 1950). Neither external morphology of the chromosomes nor the nature of chromosome association can be used as a single criterion in identifying the chromosomes of a hybrid. Therefore, whenever it is at all possible, "the form in question should be hybridized with its putative diploid ancestor or ancestors, or better yet, it should be resynthesized." However, since repeated attempts to produce hybrids between *Belladonna* and either *D. grandiflorum* or *D. elatum* have been unsuccessful and direct doubling of the chromosome number of the triploids has not been achieved, a compromise has been made in the production and study of hybrids between the triploids and Smith's *Belladonna*.

By using the triploids as female parents and pollinating them with *Belladonna* 23 F_1 seeds were obtained, of which 7 yielded plants which reached maturity. Unfortunately, these hexaploids, which are of the greatest interest in this study, are not known in as great detail as is desirable, since all but one were lost in the

TABLE VIII
MEIOSIS IN THE DERIVED HEXAPLOIDS

Plant	Chromosome Number	Metaphase I					Anaphase I				Anaphase II			
		Number of cells	Number bivalents per cell–range	Total number multivalents	Number multivalents involving intermediate chromosomes	Median number bivalents	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells
51-213-3	48, 2F	45	24–19	3	1	23	139	6	13	13.7	60	9	2	18.3
51-216-6	49, 2F	6	24–20	2	0	—	—	Largely regular			—	—	—	
51-216-10	50 (7A)	29	24–22	8	2	24	45	1	4	11.1	About 15% irreg.			
51-216-16	50 (7A)	31	24–20	4	0	24	65	9	9	27.7	—	—	—	—
51-219-4	46	55	22–17	0	0	21	50	8	2	20.0	37	2	2	11.2
51-220-4	48	10	23–20	1	0	—	25	3	2	20.0	—	—	—	—
51-221-11	48	20	24–21	0	0	23	82	8	8	19.5	70	5	13	25.7
51-222-21	47	33	23–20	1	0	21	83	17	4	25.0	45	7	5	26.6
51-222-38	48	23	24–21	0	0	23	32	7	5	37.3	22	7	3	45.4
51-223-5	47	33	23–21..	2	1	23	—	—	—	—	—	—	—	—
51-223-31	44	7	22–17	0	0		61	8	2	16.7	36	7	5	25.0

unusually severe winter of 1951-52 following their first flowering, and most of the meiotic material available for study was a few buds embedded in paraffin.

Of the plants which were surveyed, 50-20-1 (48-6-2 × Smith's *Belladonna*) formed mostly bivalents at MI, but 6–12 univalents were commonly present, and reduced chiasma frequency in the long chromosomes was observed. At first anaphase, abnormalities were observed in 28.0 per cent of the cells studied, but in only 10.0 per cent of cells at anaphase II. Pollen viability was 41.4 per cent, and a fair amount of seed was set both by selfing and by backcrossing to *Belladonna*.

51-209-1 (48-27-5 × Smith's *Belladonna*) exhibited fairly regular pairing at MI. Usually no more than 4 univalents were found, and frequently 24 bivalents were present. Anaphase I was visibly normal in about 45 per cent of all cases, and AII was somewhat more regular. Pollen viability was in the neighborhood of 85 per cent. This plant produced a heavy set of viable seed, whether selfed or further backcrossed to *Belladonna*.

51-213-1 (50-15-4 × Smith's *Belladonna*) was studied in sectioned material, in which only approximate counts could be obtained. There was apparently relatively good pairing at MI—many PMC's appeared to be quite regular, and usually no more than 4 univalents were evident. Several times, a single trivalent involving one of the larger chromosomes was observed. AI's were regular in 60 per cent of the cases, as were most of the AII's. Pollen viability was as high as 91 per cent. Again, both selfs and backcrosses to *Belladonna* proved successful. A sister seedling, 51-213-2, showed metaphase pairing with generally 2–4 univalents, the remaining chromosomes being in bivalent configurations. AI segregation in this plant appeared to be about 55 per cent normal.

51-213-3, studied in some detail (Table VIII), had at least 23 bivalents in two-thirds of the cells at MI, and both anaphase divisions were highly regular. Little trivalent formation was recorded, however.

Two other hexaploids, 51-211-1 and 51-211-2 (50-15-1 × Cliveden Beauty), could not be analyzed; of these, the former yielded a good set of seed upon selfing. The other plant was not pollinated.

The advanced generations among the derived hexaploids had their origin, as may be seen in text-fig. 2, from five F_1 individuals. Of these, two of the parental triploids had different white *elatum* parents but the same blue *grandiflorum* parent, while the triploid parent of the third line was the offspring of an azure *elatum* variety and the fragment-bearing cobalt diploid, 47031-1. In general, as will be seen, the lines derived from the last cross are distinct in cytological behavior from the other two.

Somatic Chromosome Morphology.—

Because of the number of plants represented by these populations, studies of somatic chromosomes have been restricted to root-tip counts. The total number of each of the easily identified *A* and *B* chromosomes was counted, gross morphological alterations of the chromosomes were noted, and in instances where staining was good enough, average satellite number and disposition were determined.

TABLE IX

CHROMOSOME NUMBER IN *D. BELLADONNA* AND THE DERIVED HEXAPLOIDS

Line	Hypoploids								Hyperploids								48 chromosomes	
	Aneuploid only	Fragment only	5A	5B	7A	7B	Other	Total	Aneuploid only	Fragment only	5A	5B	7A	7B	Other	Total	Fragment	Normal
51–216	0	2	0	0	0	0	7A, 7B—1	3	2	5	0	0	6	0	8A—2 7A, 7B—1	16	4	1
51–217	1	0	0	0	1	0	0	2	0	0	0	0	3	0	7A, 7B—1	4	1	2
51-218	0	4	0	1	0	0	0	5	0	9	0	0	0	1	0	10	8	3
51–219	7	0	0	1	0	0	0	8	0	0	0	0	0	0	0	0	0	4
51–220	6	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	1
51–221	5	0	1	0	0	0	0	6	4	0	0	0	0	1	0	5	0	13
51–222	8	0	0	1	0	1	0	10	5	0	0	0	2	0	8A—1	8	1	27
51–223	8	0	0	0	0	0	0	8	3	0	0	0	0	0	0	3	0	9
51–224	6	0	0	1	0	0	0	7	0	0	0	0	0	0	0	0	0	8
52–311	15	1	0	1	1	0	0	18	0	0	0	0	0	1	0	1	0	6
51–232	10	1	1	0	0	0	0	12	2	0	0	0	0	0	0	2	0	11

As to the number of satellites present, the chief difference noted among the various populations was in the expression of the *A*-SAT, which is potentially present on two of the 6 *A* chromosomes in all lines, since the triploid and the *Belladonna* parent each should have contributed one. However, while plants in the three populations descended from the 51-213 individuals usually revealed one or two satellited *A*'s, this satellite was not strongly manifested by the other populations. Apparently, this difference had its origin in the triploid parents, since, as was mentioned above, the 50-15 individuals were characterized by possessing a more "active" *A* than the other lines.

Aneuploidy is common in all populations, as it is within *Belladonna;* however, the various lines have characteristic differences (text-fig. 7, Tables IX and X). Thus, while *Belladonna* populations contain many hypoploids with as few as 41 chromosomes and only occasional hyperploids, this pattern occurred only in 51-219 and 51-220 (51-202-3 × self, and × Smith) among the derived hexaploids. A somewhat intermediate situation was found in 51-222 and 51-223 (51-209-1 × self, and × Smith) and in 51-221 (51-202-7 × 50-20-1) in which plants with 48 chromosomes were frequent and both hypoploids and hyperploids occurred. A third situation was found in lines 51-216, 51-217, and 51-218, derived from the fragment-bearing individuals 51-213-1 and 51-213-2. In these populations, hyperploid individuals were most numerous, though an occasional plant with as few as 45 or 46 chromosomes was found. In addition, the centric fragment was quite common, being found in 17 out of 24 individuals of 51-216, and 23 of 26 individuals of 51-218. In 51-217, which was a backcross to Smith's *Belladonna,* the fragment occurred in 4 of 8 individuals examined. The exact number of fragments present in each individual is not given, since the fragment does not always segregate regularly and may occasionally vary from root-tip to root-tip

TABLE X

IRREGULAR DISTRIBUTION OF CHROMOSOMES IN THE HEXAPLOIDS

Line	Number of plants	Number chromosomes deficient			Number chromosomes in excess		
		A	B	Other	A	B	Other
51–216	24	0	0	8	11	1	17
51-217	9	0	0	2	4	1	3
51–218	26	0	1	7	0	1	14
51–219	12	0	1	18	0	0	0
51–220	7	0	0	12	0	0	0
51–221	24	0	1	7	0	1	6
51–222	45	0	1	18	4	0	6
51–223	20	0	0	14	0	0	3
51–224	15	0	1	16	0	0	0
52–311	25	0	1	49	0	1	0
51–232	25	1	0	22	0	0	2
Total	232	1	6	173	19	5	51

of a given plant. It is not known to what extent it may be possible to accumulate fragments in future generations, but in samples of two F_3 populations, each of whose progenitors bore two fragments, no more than three fragments were observed in a total of fifteen individuals; on the other hand, all but one of the remainder possessed one or two fragments. Since transmission of the fragment through both the pollen and the ovule has been demonstrated (in the pollen, on the diploid and hexaploid levels, and in the ovule, on the triploid and hexaploid levels), it may well be that the failure to find many individuals with an augmented fragment number reflects some lethal effect of numerous fragments. It may be noted that the formation of isochromosomes by misdivision of the fragment, such as was noted by Darlington in *Fritillaria* (1940) and by Rhoades in *Zea* (1940) has never been observed here, although such a chromosome should be easily recognized by its distinct morphology.

Fertility of the Derived Hexaploids.—

A systematic study of all the plants has not been made, since they number now well over 1000. As has been noted above, the initial triploid × hexaploid hybrids were of good fertility. In succeeding generations (to the F_4 and various backcrosses to *Belladonna*) plants exhibiting all degrees of fertility have been found, as evidenced particularly by seed set.

Detailed meiotic studies have been made in only a few of these plants (Table VIII), but the degree of pairing has generally been found to agree well with that characteristic of *D. Belladonna*. Thus, 51-221-11 forms no more than 6 univalents and usually only 2 at MI; no multivalents were noted; and both anaphases are fairly regular. A similar situation, with slightly more numerous irregularities in the anaphases, was found in 51-222-38. In aneuploid individuals, irregularities were, to be sure, more frequent. Thus, 51-216-10 and 51-216-16, both of which possessed an *A* chromosome in excess as well as one other excess chromosome, often formed 24 bivalents, but were also characterized by low multivalent formation, chiefly involving the extra *A* chromosome. A hypoploid (51-219-4; 46 chromosomes) averaged 21 bivalents, but the anaphases were not especially irregular. As in *Belladonna*, the number of laggards at anaphase was always much less than that of univalents at metaphase.

While infertile plants have been found both among the aneuploids and among apparently normal plants with 48 chromosomes, a study of seed germinability among those plants which have set some seed shows that, on the whole, the highest number of viable seeds were produced by plants with 48 chromosomes. However, even in this group, germinability ranged from 0 to about 90 per cent, and, with one exception, the production of seed with at least 40 per cent germinability was confined to plants having 47–49 chromosomes (Table XI).

Segregation in the Derived Hexaploids.—

On the whole, each line within this group exhibits considerable uniformity by the F_3 (or equivalent) generation. However, there are few individuals in each

TABLE XI

SEED GERMINABILITY IN *DELPHINIUM BELLADONNA* AND DERIVED HEXAPLOIDS

Plant	Chromosome number	Number seeds sown	Number seedlings	% Germinability
Smith × self	48	27	21	78
Smith × Bellamosum	48 × ?	86	25	29
Lamartine × self	48	24	14	57
Lamartine × Smith	48 × 48	52	8	17
51-216-3 × self	48	4	0	0
51-216-4 × self	49, 2F	2	0	0
51-216-12 × self	48, 2F	75	15	20
51-216-13 × self	52	15	0	0
51-218-2 × self	49, F	8	3	37
51-218-9 × self	48	14	2	14
51-218-16 × self	48, 3F	42	23	55
51-218-18 × self	49, 2F	2	0	0
51-218-19 × self	46, 2F	29	18	62
51-218-29 × self	50, 2F	68	23	34
51-218-39 × self	48, F	8	2	25
51-221-2 × self	49	50	30	60
51-222-11 × self	48	3	0	0
51-222-13 × self	47	36	4	11
51-222-19 × self	48	11	0	0
51-222-28 × self	48	4	0	0
51-222-7 × self	48	200	165	82
51-222-8 × self	48	47	21	44
51-222-14 × self	48	23	17	73
51-222-36 × self	48	12	0	0
51-222-37 × self	48	32	14	44
51-222-43 × self	47	22	3	13
51-222-46 × self	48	8	1	13
51-222-50 × self	46	33	16	48
51-222-54 × self	49	20	1	5
51-222-61 × self	48	22	13	59
51-222-67 × self	48	5	0	0
51-222-77 × self	48	9	4	45
51-222-95 × self	49	15	7	47
51-222-100 × self	48	7	1	14
51-223-1 × self	49	3	0	0
51-223-21 × self	48	10	6	60
51-223-22 × self	48	15	5	33
51-223-38 × self	48	14	5	34
51-223-44 × self	47	7	0	0

group which deviate noticeably from the rest, especially in leaf shape. In only one instance (an F_3 family derived from 51-209) have more than a few individuals deviated in the direction of either *D. grandiflorum* or *D. elatum*, and the variation here is in the direction of rather more finely dissected leaves than generally occur in *D. Belladonna*. Taken as a whole, however, the general aspect of the assemblage is that of a *Belladonna* population in which a few individuals are more or less branched, shorter or taller, or with leaves more or less finely dissected than in *D. Belladonna* Hort. (pl. 10).

Color inheritance in these forms is such as to raise some interesting questions, but detailed treatment of this subject will be reserved for future consideration.

Discussion and Summary.—

Although the analysis of meiosis in the first-generation hybrids was not complete, it is still clear from the above that while somewhat more irregular than in *Belladonna*, the meiotic process does not appear to be greatly disturbed, and in only one individual (51-213-1) was the regular production of multivalents noted.

Chromosome numbers among the progeny of these plants suggest for the various crosses what homologies and disharmonies may have been operative in their parents. Crosses 51-219-, 51-220-, and 51-223- are most similar to *Belladonna* in that chiefly euploids and hypoploids were produced. In the first two of these lines, which represent the self and backcross to Smith's *Belladonna*, respectively, of the F_2 of the cross 48-6-2 × Smith's *Belladonna*, there has been no intentional building up of the *Belladonna* complement by backcrossing. Therefore, unless the introduced chromosomes of the triploid have been appreciably eliminated, no strong barriers of chromosomal differentiation appear to exist between the parental triploid and *Belladonna*. The aneuploidy thus seems to be of the same nature as in *D. Belladonna* Hort.

On the other hand, 51-223 is a first backcross to Smith's *Belladonna* of the original hybrid between 48-27-5 and Smith's *Belladonna*. Since the same hybrid when selfed gave rise to line 51-222 (in which both hyperploids and hypoploids were frequent, and in which excessive numbers of supernumerary *A* chromosomes were found), it seems in this case that occasional formation of multivalents involving the large chromosomes must occur, and perhaps that more pronounced structural differences may exist between the parental genomes than in the previous instance. The first conclusion is based on the occurrence of 4 *A* chromosomes out of a total of 10 chromosomes extra in the hyperploid individuals of line 51-222, more than three times the expectancy if this chromosome were segregated irregularly only as often as the small chromosomes, and even more unlikely as a random event if the higher chiasma frequency of this chromosome is considered.

In the absence of any indication of multivalent formation by the smaller chromosomes, it is necessary to assume that some other factor is operative in producing individuals possessing these chromosomes in excess. This may be accounted for if gametes hyperploid for these chromosomes are not at the selective disadvantage which appears to occur in *D. Belladonna*. Such an hypothesis can best be explained if certain euploid combinations in these individuals are actually deficient for necessary genetic material, which may be supplied by the extra chromosomes.

The extreme frequency of hyperploidy in the 51-213 derivatives, where hyperploids represent the bulk of the populations, seems to indicate both high multivalent formation by the *A* chromosomes, occasional multivalent formation by the *B* chromosomes, and to a greater extent than in the preceding case, the operation of some factors which favor the functioning of gametes hyperploid for the smaller

chromosomes. This is particularly true of 51-216 and 51-217, the F_2 and first backcross respectively of 51-213-1, the plant in which multivalents were noted above. That transmission of the excess large chromosomes may be through the pollen grain as well as through the egg is suggested by the fact that a comparable excess of large chromosomes was present in 51-217, the backcross line, as compared with 51-216.

As to the fertility of the derived hexaploids, it has already been noted that euploid chromosome numbers and fertility are not necessarily related, but that, on the whole, more plants which yield seeds with good germination have about 48 chromosomes than have chromosomes either much in excess or in deficiency of this number. The tendency to preserve the hexaploid number appears to be almost as strong as in the *Belladonna* lines themselves.

So far as the homologies of the genomes derived from triploid and hexaploid sources are concerned, it seems that they must be very nearly similar, since there has been no strong morphological or cytological disharmony in the derived hexaploids as compared with *D. Belladonna*. In fact, the differences are very slight indeed if one contrasts the behavior of these plants with that of the intervarietal crosses between *Belladonna* and Bellamosum. Although the latter variety was derived from the former, yet reduced seed germinability and more frequent aneuploid production have been found to occur in their hybrids than characterize either variety when it is selfed.

General Discussion

It is concluded that *D. Belladonna* Hort. is an allopolyploid hybrid between the tetraploid species *D. elatum* L. and the diploid species complex of *D. grandiflorum* L. In general, *D. Belladonna* may best be classed as a complex segmental allopolyploid, but it should be emphasized that classification is especially difficult since strong chromosomal barriers to hybridization do not seem to exist between even distantly related species of *Delphinium* (e.g., *D. elatum* and *D. nudicaule* or *D. cardinale*). Unlike many other segmental allopolyploids, however, *D. Belladonna* is easily distinguished from both parents. It has already been suggested that regularity in pairing, enforced by differential affinity of the chromosomes, as well as by the not insignificant effect of low chiasma frequency, is probably responsible in large part for this behavior. Moreover, the quantitative mode of inheritance of many of the characters tends to keep *D. Belladonna* in its intermediate morphological position between the parents.

Undoubtedly, a large part of the success of *D. Belladonna* (as opposed to the frequent failure of such hybrids to be perpetuated in nature; Clausen, Keck and Hiesey, 1945) has been the result of its being a garden plant. Thus, in the first place, it was vegetatively propagated for an unknown number of years before the first occurrence of fertility was reported; second, it has been subject to the care and selection of gardeners and plant breeders over the years, so that the difficulties (for instance, multivalent formation by the large chromosomes) such a hybrid would encounter during the first few generations in nature were mostly obviated.

Several explanations may be offered to account for the *elatum* tendencies noted in the experimentally produced triploids. First, while *D. grandiflorum* has a number of varieties, those varieties grown in gardens are, on the whole, similar with respect to the features which they contribute to the phenotype of *Belladonna*—the large self-colored bee, the wide open flower, the few-flowered inflorescence, the finely dissected leaves, and much-branched habit. *D. elatum*, on the other hand, exists in many natural and horticultural variants; probably a *D. elatum* bred for a showy "bee," with a relatively open inflorescence and rather narrow leaf segments, would yield offspring of the type characteristic of *Belladonna* when such a variety was crossed with *grandiflorum*. However, the *elatum* variety Summer Skies, seed parent of triploids 50-15, has a small bee, broad leaf segments, and very dense strong main spike with numerous flowers; the triploids plotted in text-fig. 5 are indeed intermediate with respect to their known parents. All one can say of the presumptive *elatum* parent of *Belladonna* is that it was almost certainly a smaller, less extreme variety than those grown today, judging from historical plates of Delphiniums cultivated in the middle of the last century.

The question of the nomenclature of the triploid and hexaploid garden Delphiniums may be viewed in three very different aspects: first, as it concerns the taxonomist, second, the geneticist, and third, the gardener or nurseryman. While the first two views may be reconciled to a certain extent, the unfortunate truth is that the people most concerned with these Delphiniums (which are, after all, cultivated plants) will probably perpetuate the past errors and contribute new cases of mistaken identity in the future.

For the geneticist, it is desirable that the exact parentage, insofar as it is possible, be given for every hybrid where it is known. Convenience in the herbarium, on the other hand, requires that some category be devised which will adequately contain the assemblage. Thus, according to the International Code of Botanical Nomenclature (Lanjouw, ed., 1952), "hybrids or putative hybrids between two species of the same genus are designated by a formula, and whenever it seems useful or necessary, by a name." In the latter case, the specific name is to be preceded by "×." Further, where different hybrids of the same parentage exist, they may be united in a collective taxon in which the forms are recognized as nothomorphs, "designated by an epithet preceded by the binary name of the hybrid group and the term "nothomorph." While the general practice in systematics is to give priority to the earliest validly published name, for cultivated plants provision is made that the most generally employed name may be used. Of the early names applied to hybrids of *D. grandiflorum* and *D. elatum*, only *D. formosum* and *D. Belladonna* are in wide usage. Since the name *Delphinium formosum* was given in 1856 to a wild species (Boissier and Huet), it seems advisable to maintain *D.* × *Belladonna* Hort. *ex* Bergm. (see footnote, p. 119) as the epithet of the hexaploid Delphiniums and their triploid allies. Varieties such as Lamartine, Capri, *Moerheimi*, and the triploids and derived hexaploids of this study may then be considered as nothomorphs of this species.

Summary

1. Previous workers have postulated that *D. Belladonna* Hort. originated either as a variety of *D. cheilanthum* Fisch. *ex* DC., or as a hybrid of *D. cheilanthum* with some unknown other species, or by hybridization between such diploid and tetraploid species as *D. grandiflorum* L. and *D. elatum* L. It is pointed out that solution of the problem must be based upon a combination of methods, including historical research, morphological analysis, and cytogenetic data.

2. A study of the taxonomic and horticultural literature indicates that *D. cheilanthum* is a coherent diploid species, rare in gardens, native to Siberia, Mongolia, and Kumaon (China), with relatives in adjacent areas; *D. Belladonna*, on the other hand, is a hexaploid, known only in gardens, where it has arisen upon different occasions.

3. Hybrids between various lines of *D. elatum* and *D. grandiflorum* var. *chinensis* have been produced and have been found to be morphologically comparable to *D.* × *Belladonna* Hort. *ex* Bergm. and, moreover, within the limits imposed by their triploid condition, interfertile with the "species."

4. Character analysis of the various species and hybrids indicates that both *Belladonna* and the experimentally produced triploids are intermediate with regards to *D. elatum* and *D. grandiflorum*, but that *D. cheilanthum* is morphologically and cytologically distinct from *D. Belladonna* and could not have been the diploid parent of the latter if *D. elatum* was the tetraploid parent.

5. Methods are given for the study of somatic and meiotic chromosomes and of pollen mounts.

6. It is pointed out that for the species and hybrids studied, size of pollen grain may be used as an indicator of polyploid level in both living plants and herbarium material.

7. Study of the morphology of the somatic chromosomes has shown that the genomes of the two diploid types which have been considered possible parents of *D. Belladonna* may de distinguished on the basis of their satellite distribution. In *D. grandiflorum*, satellites occur on chromosomes *C* and *H*, while in *D. cheilanthum* the *A* and the *C* chromosomes are satellited. Further, the length of the satellited arm of chromosome *A* in *D. cheilanthum* is longer than the corresponding arm of the same chromosome in *D. grandiflorum*, suggesting that there has been a translocation of the satellite-bearing segment in the evolution of the genome.

8. Differential activity of the satellites was found to characterize even the diploid species: in *D. grandiflorum* the *C* satellite is about twice as "active" as the *H* satellite; in the closely related *D. tatsienense*, both are equally active. In *D. cheilanthum* the *A* satellite is about twice as active as the *C* satellite.

9. The tetraploid species *D. elatum* was found to have a gametic complement corresponding to the summation of the *grandiflorum* and the *cheilanthum* genomes. Amphiplasty of the *H* satellite occurs.

10. In all of the experimentally produced triploids the potential satellite number was found to be 1 *A*, 3 *C*'s, and 2 *H*'s, but in triploids of lines 48-27 and

48-6, the *A* satellite was rarely evident on account of amphiplasty. The morphology of the chromosomes of *Belladonna* supports the hypothesis of similar parentage for these types, since the total *Belladonna* complement has double the potential satellite number of the triploids. In both the triploids and in *Belladonna*, amphiplasty of the *A* satellite was found in some individuals.

11. Meiosis in *D. grandiflorum* and *D. elatum* is largely regular, the chromosomes forming bivalents (rarely some univalents in the latter species) and assorting on the whole regularly.

12. In the triploid hybrids, prophase and metaphase pairing is chiefly in univalents and bivalents, trivalents being formed only rarely and only by the *A* or *B* chromosomes. Chiasma frequency is somewhat reduced and both intergenomal and intra-genomal pairing of the chromosomes occurs. Bridges and fragments are characteristic of both anaphase divisions, although the number of chromosomes lagging at anaphase is considerably less than that of univalents at metaphase. Micronuclei are frequent, and rare viable unreduced pollen grains are produced.

13. Meiosis in *Belladonna* is more or less regular, but the production of univalents commonly occurs, and aneuploid gametes are produced and function. Chromosome numbers as low as 41 have been found, but ordinarily only those plants with about the hexaploid number are fully fertile. It is suggested that *D. Belladonna* is a segmental allopolyploid which preserves a uniform appearance because low chiasma frequencies of the chromosomes enforce bivalent formation and because of the quantitative mode of inheritance of many characters.

14. Lines of derived hexaploids have been produced by pollinating various triploids with pollen of Smith's *Belladonna*, and further selfing or backcrossing of the plants produced. On the whole, these lines are only slightly more variable than is *D. Belladonna*, and fertility is only slightly impaired as compared with that "species." A small amount of multivalent formation characterizes some of these lines.

15. It is concluded that *D.* × *Belladonna* Hort. *ex* Bergm. embraces the entire assemblage of present-day varieties derived from crossing *D. elatum* with *D. grandiflorum*, as well as a number of hybrids of the last century which are no longer in cultivation.

16. A telocentric fragment has been transmitted from a *D. grandiflorum* pollen parent through four generations. No isochromosomes have been observed.

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Appendix

Chromosome numbers occurring in the species of *Delphinium*

Species	2n number	Author and date
Ajacis L.	16	Langlet, 1927; Tjebbes, 1927; Gregory, 1941
Andersoni Gray	16	Lewis *et al*, 1951
azureum Michx.*	32?	Lewitsky, 1931; Gregory, 1941
Belladonna Hort.	48	Langlet, 1927; Lawrence, 1936; Propach, 1939, 1940
Blochmanae Greene	16	Lewis *et al*, 1951
brachycentrum Ledeb.	16	Langlet, 1932
Brunonianum Royle	16	Lewitsky, 1931; Propach, 1940
bulleyanum Forrest	32	Gregory, 1941
californicum T. & G.	16	Lewis *et al*, 1951
cardinale Hook.	16	Propach, 1940; Mehlquist, 1943; Lewis *et al*, 1951
cardiopetalum D.C.	16	Tjebbes, 1927; Lewitsky, 1931; Gregory, 1941
carolinianum Walt.*	32?	Gregory, 1941
cashimirianum Royle	16	Propach, 1940
caucasicum C. A. Mey.	16	Gregory, 1941
cheilanthum Fisch. *ex* DC.	16	Propach, 1939
Consolida L.	16	Hocquette, 1922; Tjebbes, 1927; Langlet, 1927; Lewitsky, 1931; Gregory, 1941
cuyamacae Abrams	16	Lewis *et al*, 1951
decorum Fisch. and Mey, ssp. *Tracyi* Ewan	16	Lewis *et al*, 1951
Delaveyi Franch.	16	Lewitsky, 1931; Propach, 1940
Dubmbergi Huth	32	Lewitsky, 1931
elatum L.	16	Propach, 1940
fissum Waldst. & Kit.	32	Lewitsky, 1931; Propach, 1940; Gregory, 1941
flexuosum Raf.	32	Hocquette, 1922; Propach, 1940
formosum Boiss. & Huet.	32	Gregory, 1941
gayanum Willmott	32	Gregory, 1941
glaucum Wats.	16	Gregory, 1941
gracilentum Greene	16	Lewis *et al*, 1951
grandiflorum L.	16	Lewis *et al*, 1951
	16	Propach, 1940

*Mehlquist (unpublished) has determined these American species as diploid. His studies were of plants from the native habitat, whereas the other determinations were probably made from material sent out from European botanical gardens, which often confuse *D. elatum* with *D. carolinianum* and *D. azureum*.

Species	2n number	Author and date
gypsophilum Ewan	16, 32	Lewis *et al*, 1951
Hanseni Greene	16, 32	Lewis *et al*, 1951
hesperium Gray	16	Lewis *et al*, 1951
hesperium f. *pallescens* Ewan	16	Lewis *et al*, 1951
iliense Huth	16	Propach, 1940
inopinum (= *D. parishii* var. *inopinum* Jeps.)	16	Lewis *et al*, 1951
Lamartine Hort.	48	Lawrence, 1936
Moerheimii Hort.	24	Lawrence, 1936
nudicaule Torr. & Gray	16	Tjebbes, 1927; Propach, 1940; Gregory, 1941; Lewis *et al*, 1951
Nuttallianum Pritz.	16	Lewis *et al*, 1951
orientale (?) (*D. orientale* Losc.; *D. orientale* S. Gay)	16	Beckman, 1928; Gregory, 1941
Parishii Gray	16	Lewis, *et al*, 1951
Parryi Gray	16	Lewis, *et al*, 1951
Parryi ssp. *seditiosum* (Jeps.) Ewan	16	Lewis, *et al*, 1951
patens Benth.	16	Lewis, *et al*, 1951
Penardi Huth	16	Gregory, 1941
peregrinum L.	16	Gregory, 1941
pictum Willd.	16	Gregory, 1941
polycladon Eastw.	16	Lewis *et al*, 1951
Purpusii Brandg.	16	Lewis *et al*, 1951
recurvatum Greene	16	Lewis *et al*, 1951
Ruysii Hort	32	Lawrence, 1936
scopulorum Gray	16	Gregory, 1941
speciosum (?) (*D. speciosum* Janka = *D. elatum* L.; *D. speciosum* Bieb.)	16	Langlet, 1927
Staphisagria L.	16	Hocquette, 1922; Langlet, 1927; Lewitsky, 1931; Gregory, 1941
sulphureum Boiss. & Hausskn	16	Gage, this paper
tatsienense Franch.	16	Lewitsky, 1931; Propach, 1940
tricorne Michx.	16	Gregory, 1941
trolliifolium Gray	16	Lewis *et al*, 1951
truncatum Lang.	16	Langlet, 1927
uliginosum Curran	16	Lewis *et al*, 1951
umbraculorum nom. nud.	16	Lewis *et al*, 1951
variegatum Torr. & Gray	16, 32	Lewis *et al*, 1951
yunnanense Franch.	16	Gregory, 1941
Zalil Aitch. & Hemsl.	16	Gage, this paper

CHROMOSOME NUMBERS OCCURRING IN THE HYBRIDS DETERMINED BY H. PROPACH, 1940

Variety	Breeder or Source	Chromosome Number
Eisberg	E. Benary, Erfurt	16
Blauglut	K. Foerster, Bornim	24
Blautanne	"	24
Alpenbote	"	32
Berghimmel	"	"
Blaurake	"	"
Blickfang	"	"

Dein blaues Wunder	K. Foerster, Bornim	32
Enzianherold	"	"
Enzianturm	"	"
Ernst von Borsig	"	"
Fön	"	"
Glasfenster	"	"
Gletscherwasser	"	"
Gnom	"	"
Grossenwahn	"	"
Gute Nacht	"	"
Havelland	"	"
Kirchenfenster	"	"
Kreuzritter	"	"
Lautsprecher	"	"
Leuchtturm	"	"
Morgenstrahl	"	"
Münsterturm	"	"
Nachtauge	"	"
Nachthorn	"	"
Nostradamus	"	"
Opalsäule	"	"
Perlmutterbaum	"	"
Purpurritter	"	"
Rosenquarz	"	"
Sontagskind	"	"
Stichflamme	"	"
Tante Clothilde	"	"
Tempelgong	"	"
Troppenacht	"	"

Explanation of Plate

PLATE 7

Fig. 1. *Delphinium cheilanthum* Fisch., reproduced from von Schrank, 'Plantae Rariores Horti Academici Monacensis,' pl. 52. 1819.

Fig. 2. *Delphinium Hendersoni*, from Revue Horticole. 1854.

GAGE—DELPHINIUM - BELLADONNA HORT.

Explanation of Plate

PLATE 8

Fig. 1. *Delphinium Belladonna*, Smith's selection from "Cliveden Beauty."

Fig. 2. *Delphinium formosum*, from Flore des Serres. 1857.

Explanation of Plate

PLATE 9

Figs. 1 and 2. Habit and detail of inflorescence of *Delphinium cheilanthum* Fisch. *ex* DC., grown at the Missouri Botanical Garden from seed received from Uppsala.

Figs. 3 and 4. Habit and detail of *Delphinium grandiflorum* L. var. *chinensis* Fisch., "Blue Butterfly."

1 2 3 4

GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 10

Figs. 1 and 2. Inflorescence and detail of chimaeric derived hexaploid 51-222-7.

Fig. 3. *Delphinium elatum* L. Plant 47-98-3, seed parent of the 48-27 series of triploids.

Explanation of Plate

PLATE 11

Triploid 48-27-3 (1), habit, (2), detail.

1 2

GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 12

Figs. 1 and 2. Habit and detail of *Delphinium elatum* L., horticultural variety "Summer Skies," seed parent of lines 50-15 and 50-40.

Figs. 3 and 4. Inflorescence and detail of triploid 50-15-4.

1

2

3

4

GAGE—DELPHINIUM × BELLADONNA HORT.

EXPLANATION OF PLATE

PLATE 13

Photographs, × 1600; camera-lucida drawings, × 1450.

Fig. 1. Ideogram of the haploid chromosome complement of *D. grandiflorum* var. *chinense*, horticultural form "Blue Butterfly."

Fig. 2. Ideogram of the haploid chromosome complement of *D. cheilanthum*.

Fig. 3. Photograph of somatic metaphase of a white variety of *D. grandiflorum* var. *chinense*, showing satellites on one *C* and two *H*'s.

Fig. 4. Photograph of somatic metaphase of the same plant, showing heterochromatic regions as well as three of the satellites.

Fig. 5. Somatic metaphase of *D. cheilanthum*, showing the four satellited chromosomes.

Fig. 6. Camera-lucida drawing of the cell in fig. 5.

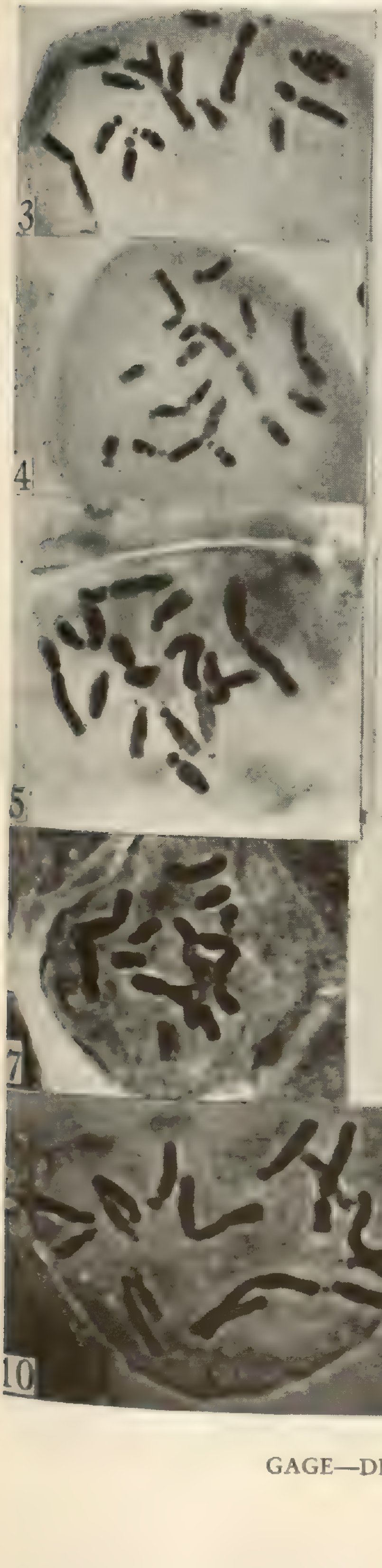
Fig. 7. Photograph of metaphase chromosomes of "Blue Butterfly" from a root-tip preparation.

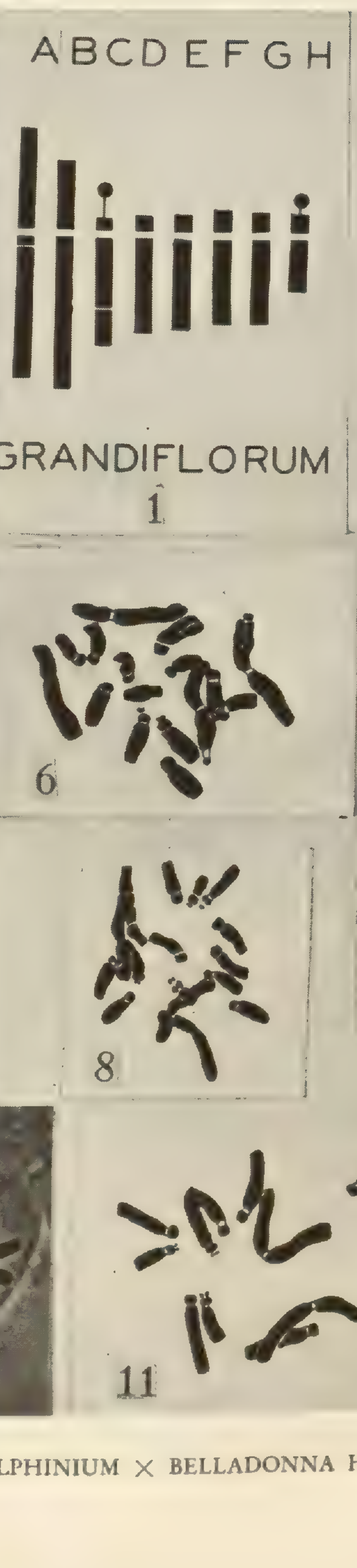
Fig. 8. Camera-lucida drawing of somatic chromosomes of "Blue Butterfly" showing satellites on both *C*'s and both *H*'s.

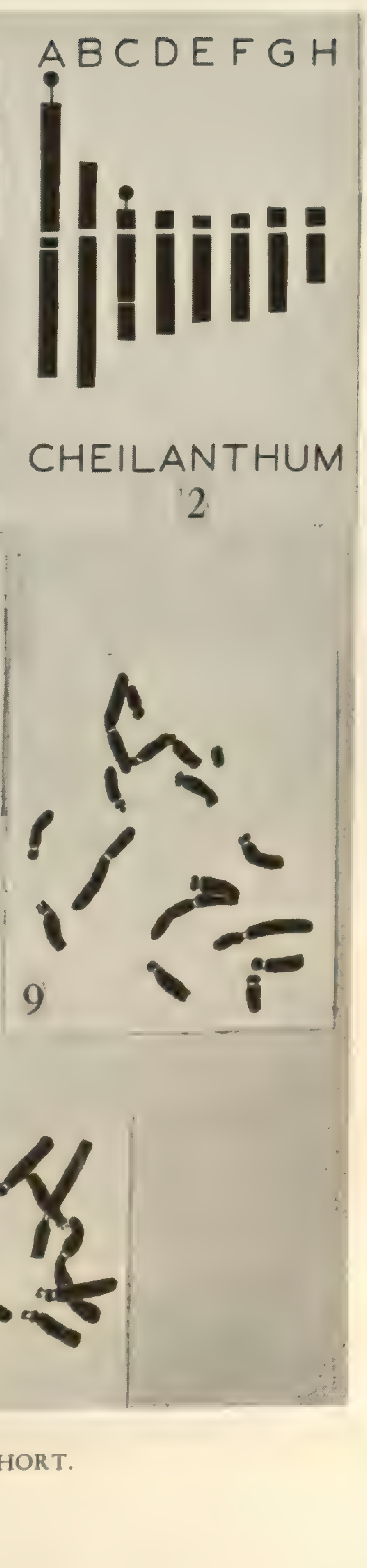
Fig. 9. Camera-lucida drawing of somatic metaphase of 47031-1, showing fragment.

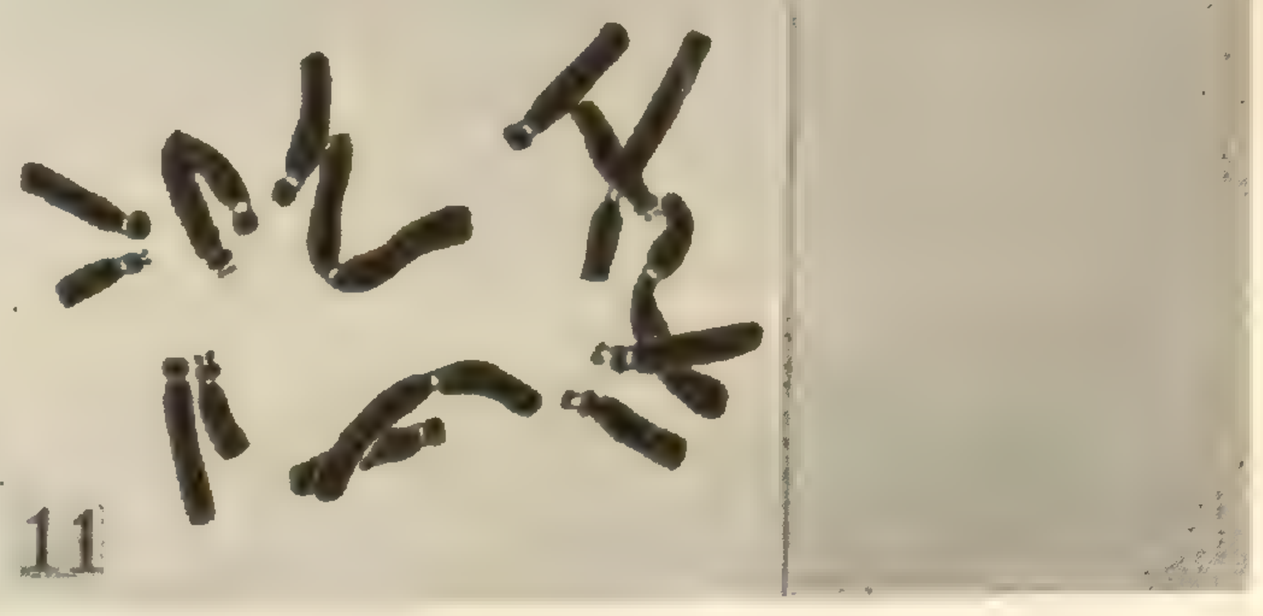
Fig. 10. Somatic complement of *D. cardinale* showing satellites on six chromosomes of the diploid complement.

Fig. 11. Drawing of the cell in fig. 10.









GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 14

Magnification of photographs as indicated; camera-lucida drawings, × 1350.

Fig. 1. Photograph of somatic chromosomes of 48-27-2. × 1500.

Fig. 2. Drawing of the cell in fig. 1.

Fig. 3. Camera-lucida drawing of the chromosomes in a root-tip preparation of 48-6-2, showing satellites on one *A*, three *C*'s, and one *H*.

Fig. 4. Drawing of the somatic chromosomes of "Summer Skies," showing satellites on two *A*'s, two *C*'s, and two *H*'s.

Fig. 5. Camera-lucida drawing of the somatic chromosomes of tetraploid 47-98-3. Satellites visible on two *A*'s, three *C*'s, and two *H*'s.

Fig. 6. Photograph of the cell in fig. 7. × 1500.

Fig. 7. Camera-lucida drawing of MI of triploid 48-27-3, showing 8 II and 8 I.

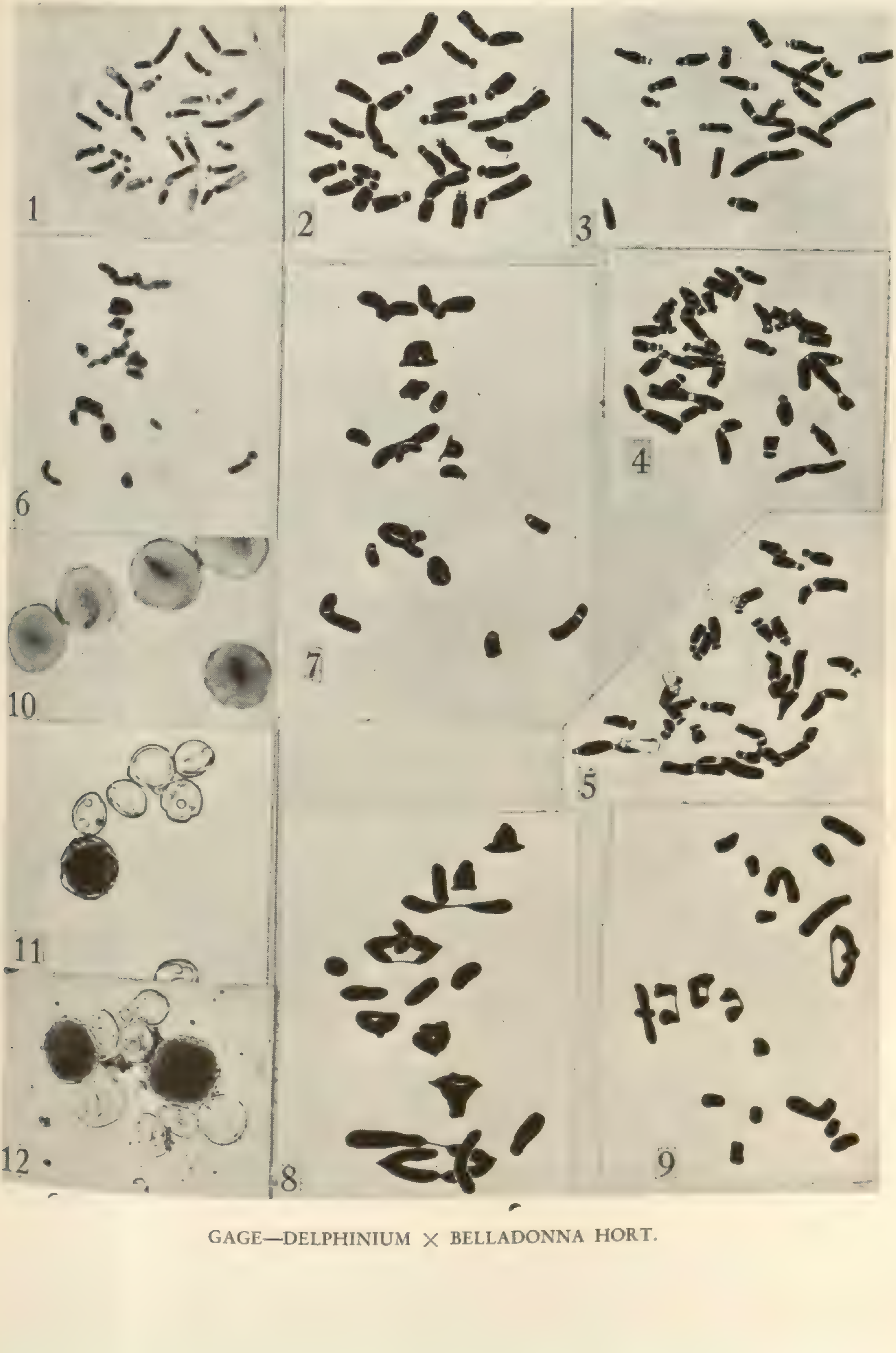
Fig. 8. MI of triploid 48-27-5, showing maximum amount of pairing observed: 1 III, 7 II, and 7 I. Five bivalents of the intermediate chromosomes have two chiasmata.

Fig. 9. MI of triploid 48-27-5, showing greatly reduced pairing: 5 II and 14 I.

Fig. 10. Pollen of "Cliveden Beauty." Pollen mostly viable. × 350.

Fig. 11. Pollen of triploid 48-6-1, showing one unreduced grain. × 350.

Fig. 12. Pollen of 50-20-1, an F_1 between Smith's *Belladonna* and triploid 48-6-2, showing aborted pollen grains. × 350.



GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 15

Photographs, × 1600; camera-lucida drawings, × 1450.

Fig. 1. Diakinesis and early metaphase I of "Blue Butterfly," showing eight II's.

Fig. 2. Photograph of the somatic chromosomes of *D. Belladonna*.

Fig. 3. Anaphase I of 47031-1 with lagging fragment.

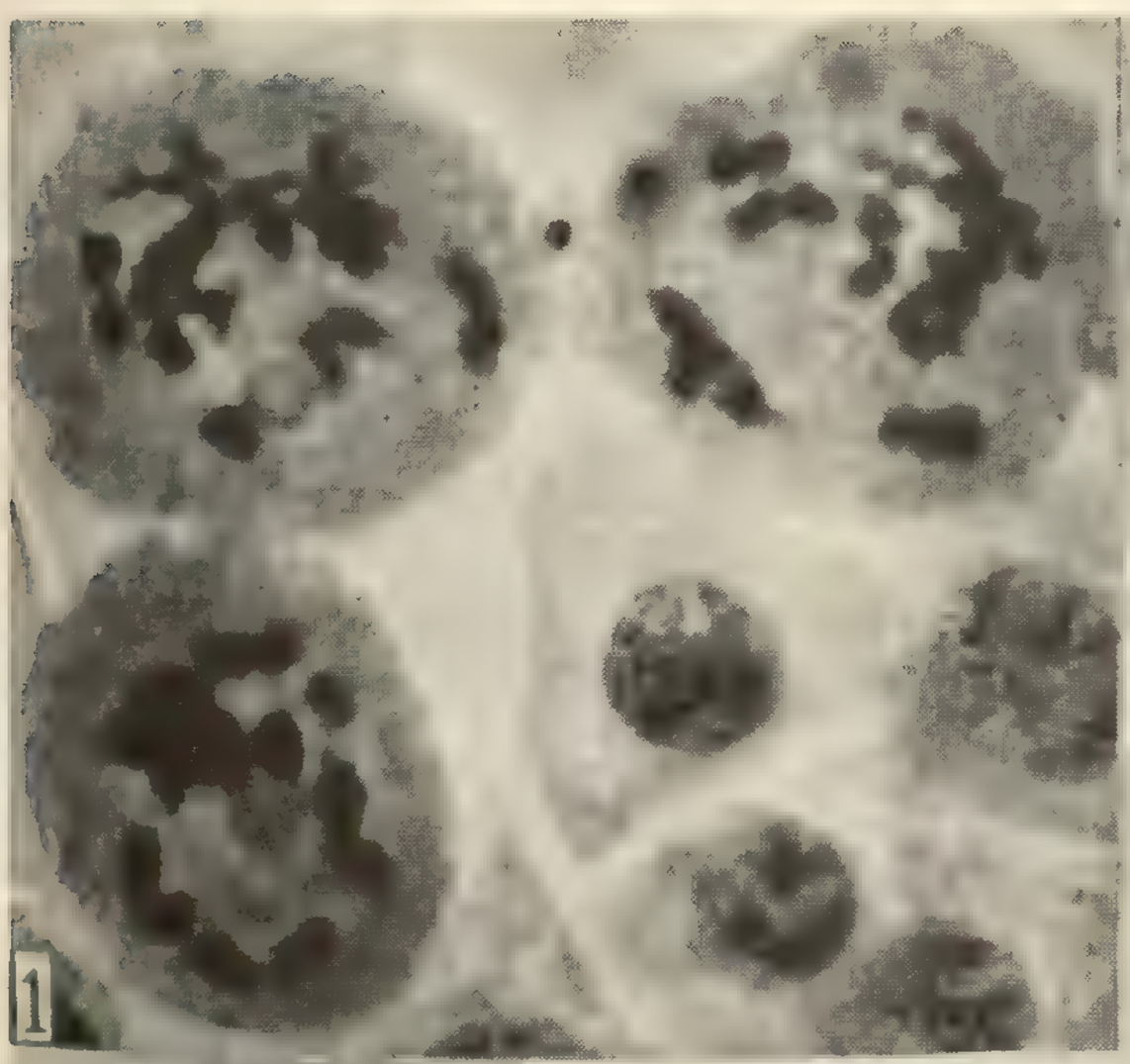
Fig. 4. Diakinesis of "Summer Skies," showing essentially regular pairing.

Fig. 5. Photograph of MI of Smith's *Belladonna*, showing eight univalents and only two of the large bivalents with two chiasmata. This was among the most extreme cases of lack of pairing observed in this plant.

Fig. 6. Drawing of the cell in fig. 2, showing satellites on one *A*, six *C*'s, and one *H*.

Fig. 7. Camera-lucida drawing of diakinesis of Smith's *Belladonna*, showing six univalents.

Fig. 8. Camera-lucida drawing of the cell in fig. 5.



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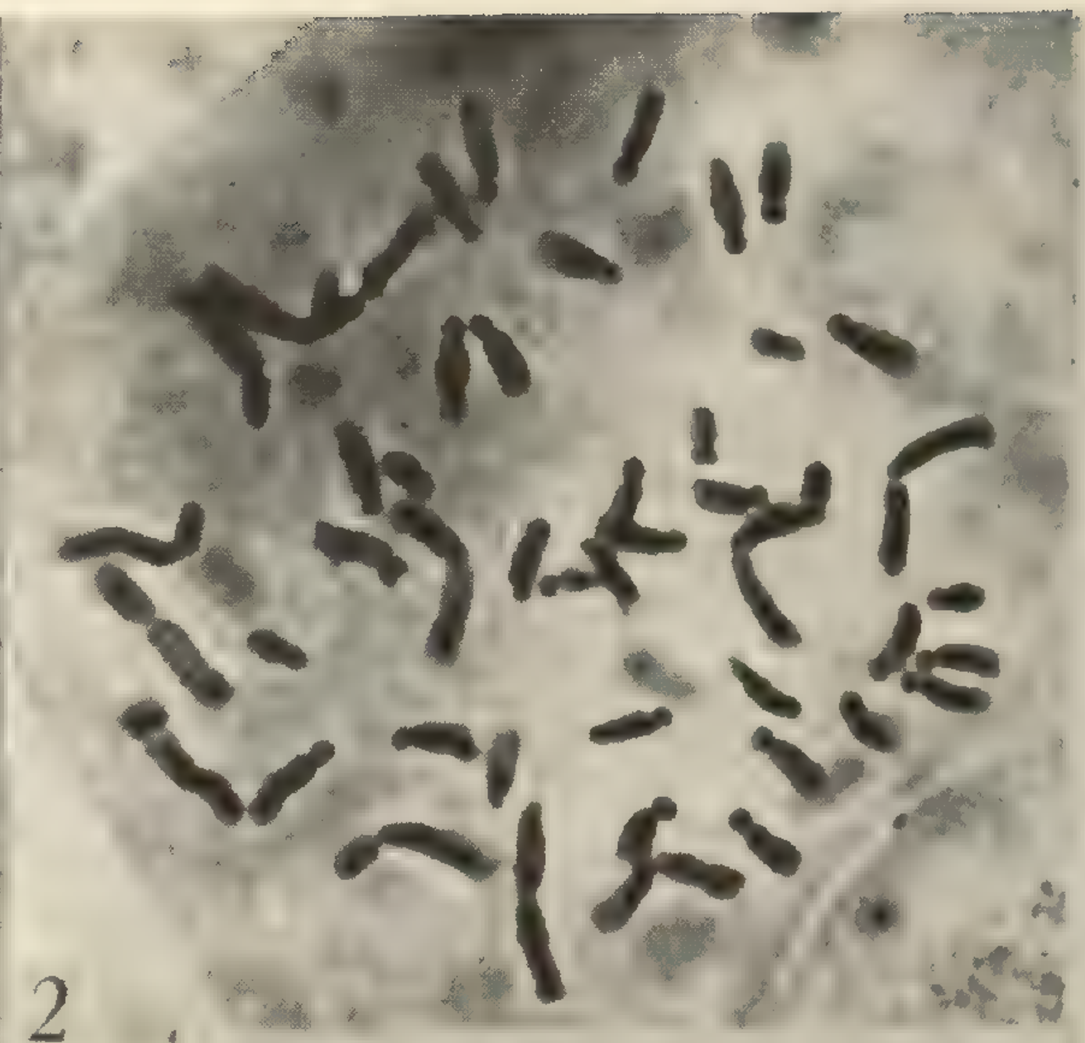

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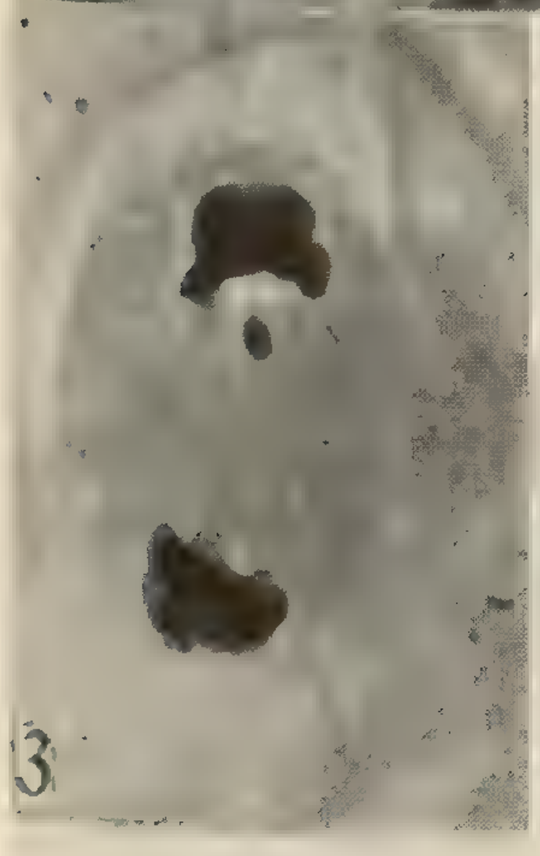

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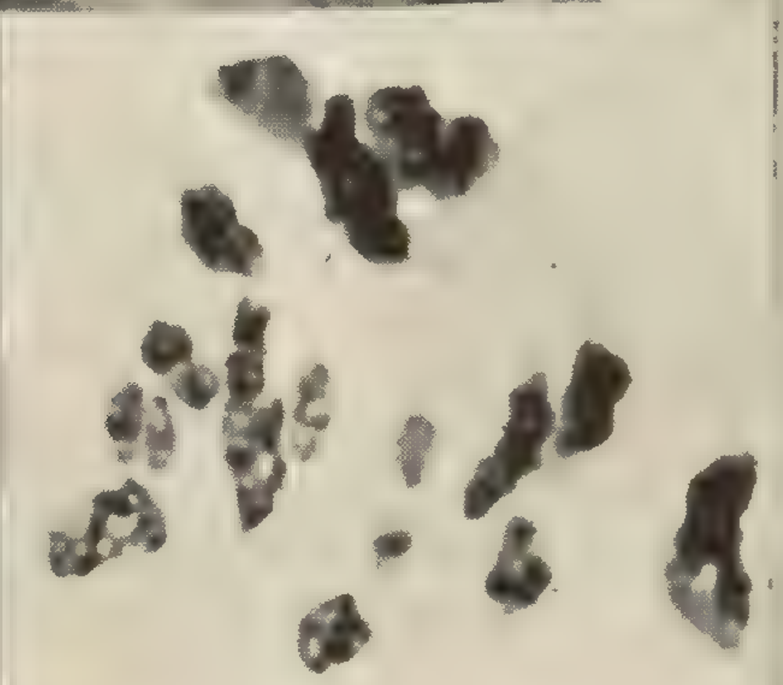

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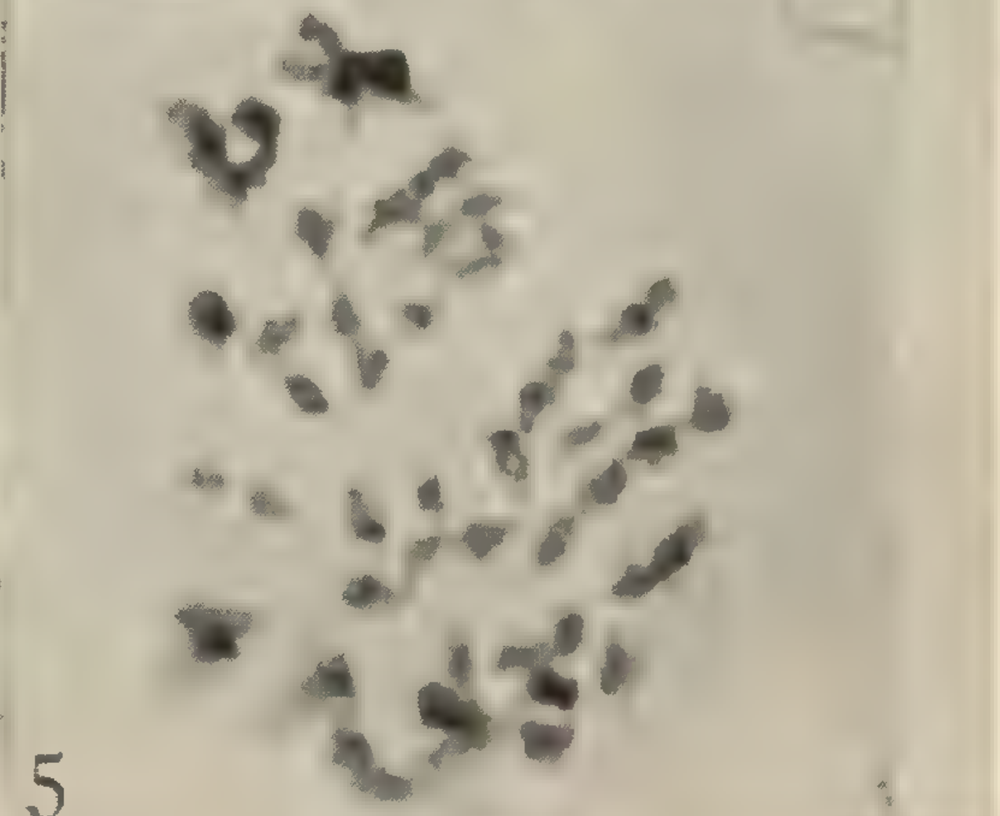

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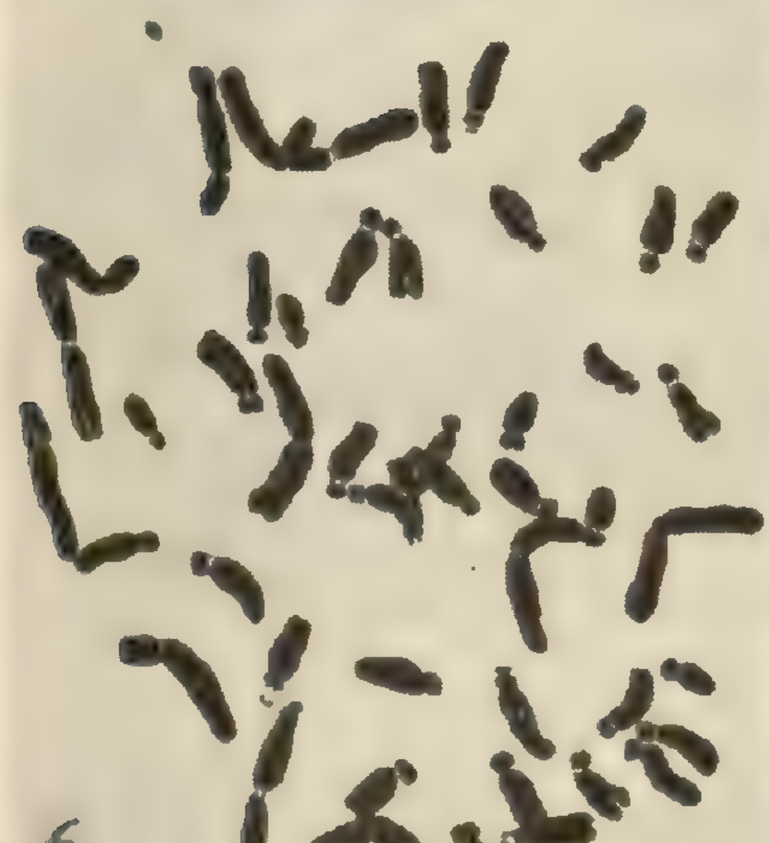

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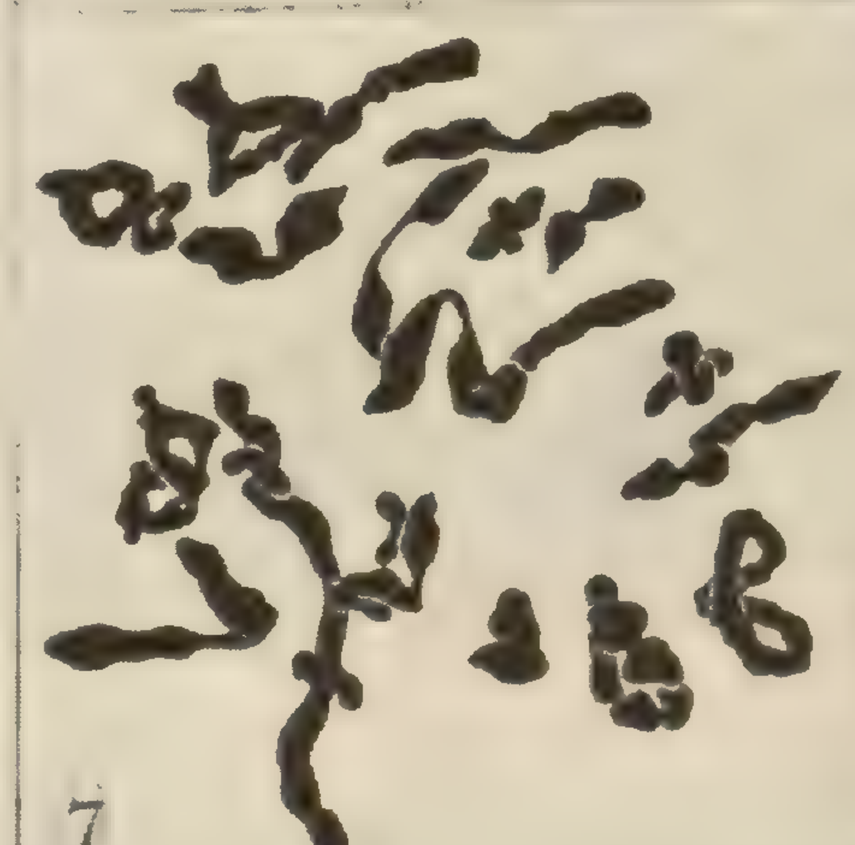

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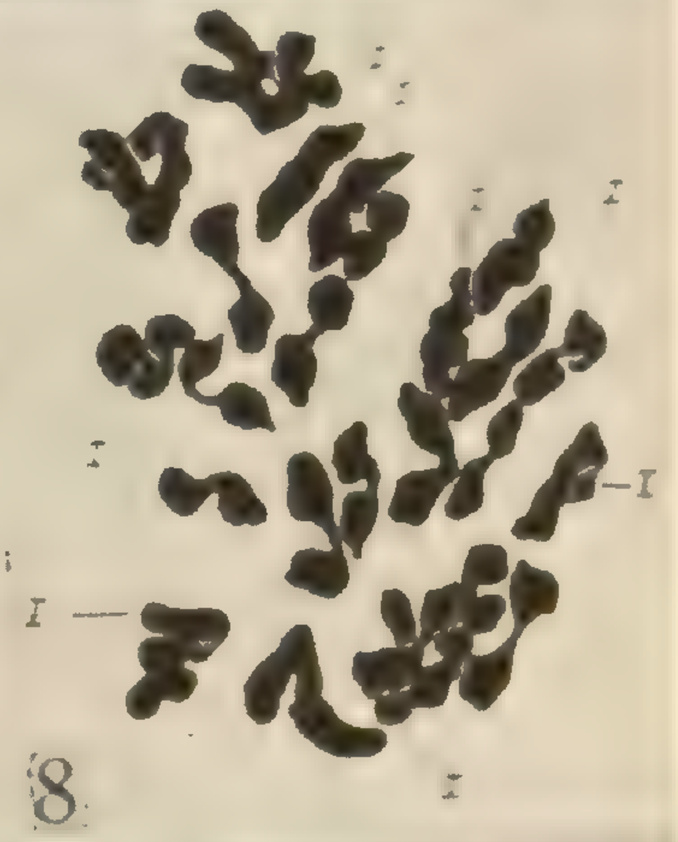

8

GAGE—DELPHINIUM × BELLADONNA HORT.

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Some American Medullosas . . . . . Henry N. Andrews and Sergius H. Mamay 183–209
The Distribution of *Diospyros virginiana* L. . Harry R. Skallerup 211–225
Wildwood—A Study in Historical Ecology . . Alfred G. Etter 227–258

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Annals
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Vol. 40 SEPTEMBER, 1953 No. 3

SOME AMERICAN MEDULLOSAS[1]

HENRY N. ANDREWS AND SERGIUS H. MAMAY[2]

The continued discovery of new species of the polystelic stems referable to the genus *Medullosa* emphasizes the conspicuous role that these plants played in the Pennsylvanian floras of the United States. Almost every large collection of coal balls that is studied reveals a specimen or two that differs in some way from those previously described. Although it has been impossible to define species limits with definite clarity when the specimens are fragmentary, poorly preserved, or represent only a short segment of the stem, it seems more than likely that most recorded American species are valid.

Those of us who have worked with these plants assumed some time ago that as the sources of material were more extensively explored our efforts would tend toward working out fine details rather than reporting ever more bizarre forms. Actually the reverse has proved to be the case, and the occurrence in recent collections of specimens of greater stem length has permitted more satisfactory study of variable characters such as stelar number.

One of the most notable contributions to our knowledge of the Medullosas is the recent description of M. *heterostelica* by Stewart and Delevoryas (1952). Although it is a bi-stelar stem the two steles divide in the nodal region to form a complex of twenty or more, some of which contribute to the petiole traces, whereas others reunite, the stem becoming bi-stelar again above the node. Had this specimen been found in a more fragmentary condition, descriptions of several "species" might well have resulted. As it is, the evidence suggests that stelar number is a reliable taxonomic character provided that a representative specimen of the stem is available.

The present account deals with several *Medullosa* specimens that have come to light in the paleobotanical laboratory of Washington University since Baxter's contribution in 1949. Certain of these add to our knowledge of the distribution of previously described species; others are distinctly new and present what we

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[1] Publication authorized by the Director, U. S. Geological Survey.

[2] U. S. Geological Survey, Washington 25, D. C.

Issued September 30, 1953.

believe to be highly significant information bearing on the problem of the taxonomic significance of stelar number.

MEDULLOSA THOMPSONII Andrews

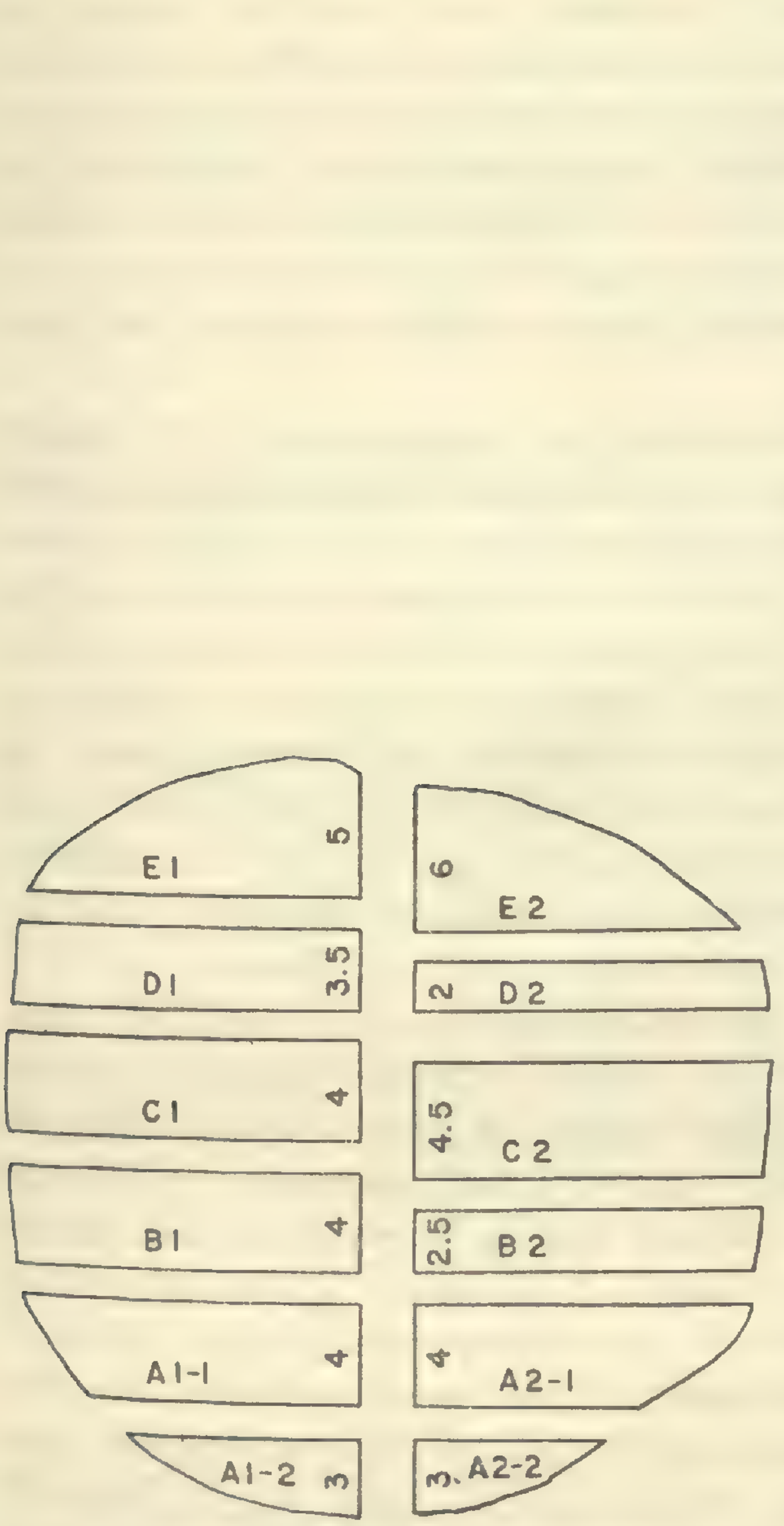
Two specimens referable to this species are present in our collections; both come from southeastern Kansas. One (No. 721) presents three steles (fig. 2), measuring 5 × 2.5 mm., 6 × 2.5 mm., and 2 mm. in diameter respectively and compares closely with the type specimen described from Iowa (Andrews, 1945). The second specimen is of interest because of its length and the type of stelar changes that occur. This stem, found in coal ball No. 713, is approximately 23 cm. long. No recognizable plant remains were evident on the exterior of the coal ball to guide the initial cut, and by chance the stem was dissected in a nearly median longitudinal plane. This seemed unfortunate at first, although it has materially aided us in following the changing stelar morphology through the length of the specimen. The plane of this initial cut accounts for the conspicuous break in certain of the cross-section illustrations (figs. 5-7).

Text-figures 1 and 2 show, respectively, a profile of the coal ball and a sketch of the stelar system indicating the divisions and fusions that take place. In the A1-2 and A2-2 blocks three steles (fig. 6) are present. These are enclosed by a clearly defined internal periderm that does not exceed 0.5 mm. in width and consists of rather thin-walled nearly cubical cells that present essentially the same appearance in transverse and radial sections. The steles at this point measure 13 × 9.5 mm., 11.5 × 6 mm., and 20 × 7 mm. In passing through the A1-1 and A2-1 blocks two of the steles fuse; the resultant two steles (fig. 7) measure 14 × 7.3 and 21.5 × 8 mm. Further divisions and fusions are indicated in text-fig. 2 as follows: In passing through the B blocks a stele divides, revealing three steles on the upper surface; in passing through the C blocks a fusion takes place, revealing two steles on the lower surface of D1 and D2; finally a small stele separates from one of the two steles, revealing three steles on the lower surface of the E blocks. Although the phloem is partly preserved, all stelar dimensions refer to the wood only.

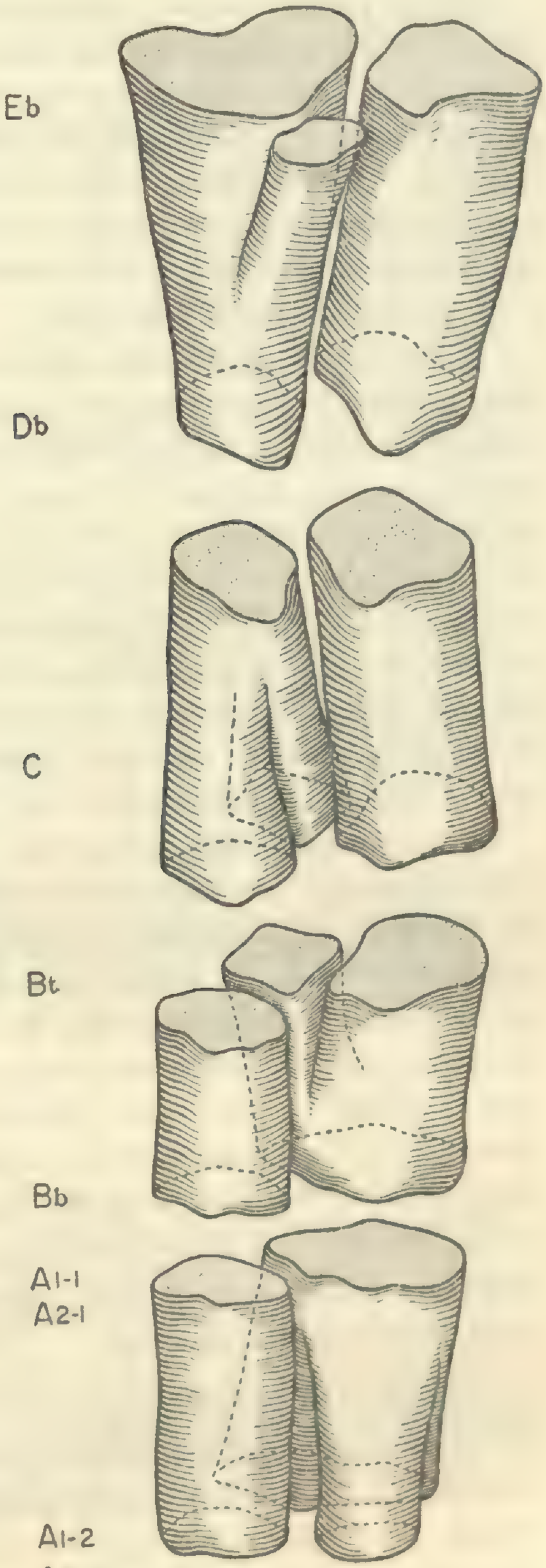
The secretory canals, which average about 0.3 mm. in diameter, are confined chiefly to the fiber zone of the cortex.

The primary body (fig. 3) contained a considerable amount of parenchyma, although this has decayed for the most part, leaving only the primary tracheids. The departing primary petiole strands are large and accompanied by little or no secondary wood. Through the length of this specimen there are at least two petioles that depart from the stem. It is especially important to note this, since obviously the type of nodal anatomy here is quite in contrast with that described for *Medullosa heterostelica*. This point will be considered in further detail under the description of the specimen that we are assigning to *M. heterostelica*.

The affinities of this stem seem to lie closest to *Medullosa distelica*, *M. anglica*, and *M. thompsonii*, but particularly the last. It differs from *M. distelica* in that



Text.-fig. 1. Profile of coal ball No. 713 containing specimen of *Medullosa thompsonii*. Numbers indicate thickness of blocks in centimeters.



Text-fig. 2. Restoration of the stelar system of *Medullosa thompsonii* (No. 713). Letters refer to the approximate position in the profile (text-fig. 1).

it presents a less constant association of secretory canals and fiber strands; an internal periderm which attains only about one-third to one-fifth the thickness of that of *distelica*; and in the stelar system the endocentric development of the secondary wood is not nearly so strongly pronounced nor as constant in our specimen. In comparing it with M. *anglica* it also appears to possess less abundant secretory canals associated with the fiber strands (Scott, 1899, pl. 12, fig. 14), somewhat smaller steles, and the secondary wood around the departing leaf traces is not retained in the Kansas fossil.

Almost every Medullosan stem discovered in American coal balls displays characteristics which tempt one to set up a new specific entity, or which at least render it difficult to assign the specimen with confidence to an established species. The four species assigned by Schopf (1939) to his subgenus *anglorota* as well as M. *thompsonii* (Andrews, 1945) and the species described more recently by Baxter (1949) are certainly all closely related. With some species the relationship is so close as to render very problematical the dividing line between species and varieties; we refer here to such specimens as M. *anglica* and its varietal forms (var. *thiesseni*, Schopf, 1939; var. *ioensis*, Andrews and Kernen, 1946), M. *thompsonii*, M. *elongata*, and M. *distelica*. Distinctive characters are somewhat more pronounced in certain others such as M. *endocentrica* and M. *primaeva*.

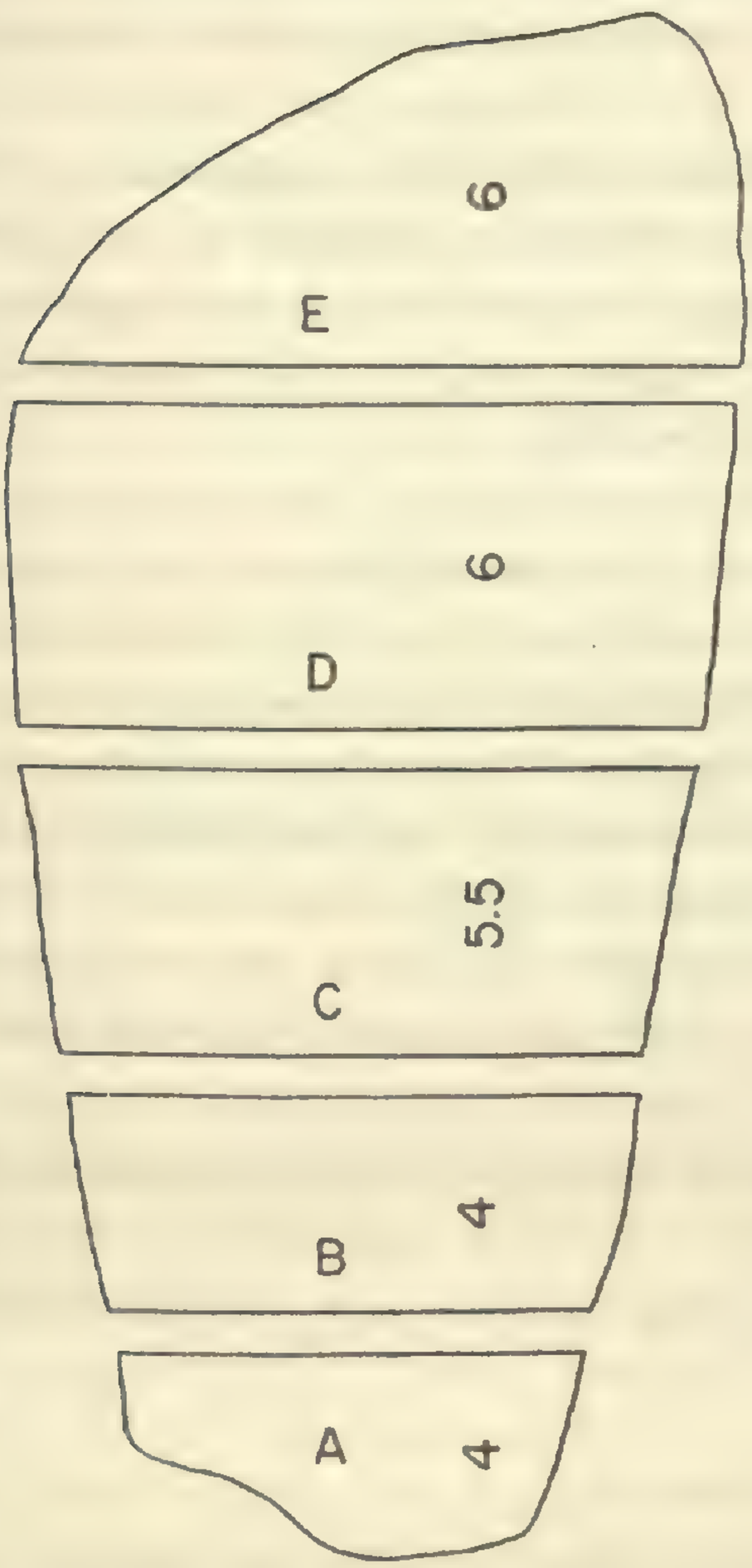
The taxonomic treatment of the specimen described above is admittedly somewhat arbitrary. Its affinity lies with the *anglica-distelica-thompsonii* complex, and the most expedient way of handling it appears to be to assign it to the last species mentioned. It differs from previously described specimens of this species only in its somewhat larger size. It is of real interest, however, for the information it conveys regarding the stelar anatomy. A seemingly significant length of stem is present to give some indication of what characters may be taxonomically dependable. Some variation in the centricity of the secondary xylem is evident, but it could at no point be closely compared with the extreme excentricity found in M. *distelica* and M. *endocentrica*. Within certain limits, which admittedly cannot be defined quantitatively, the degree and form of excentricity in *Medullosa* stems appear to be significant.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

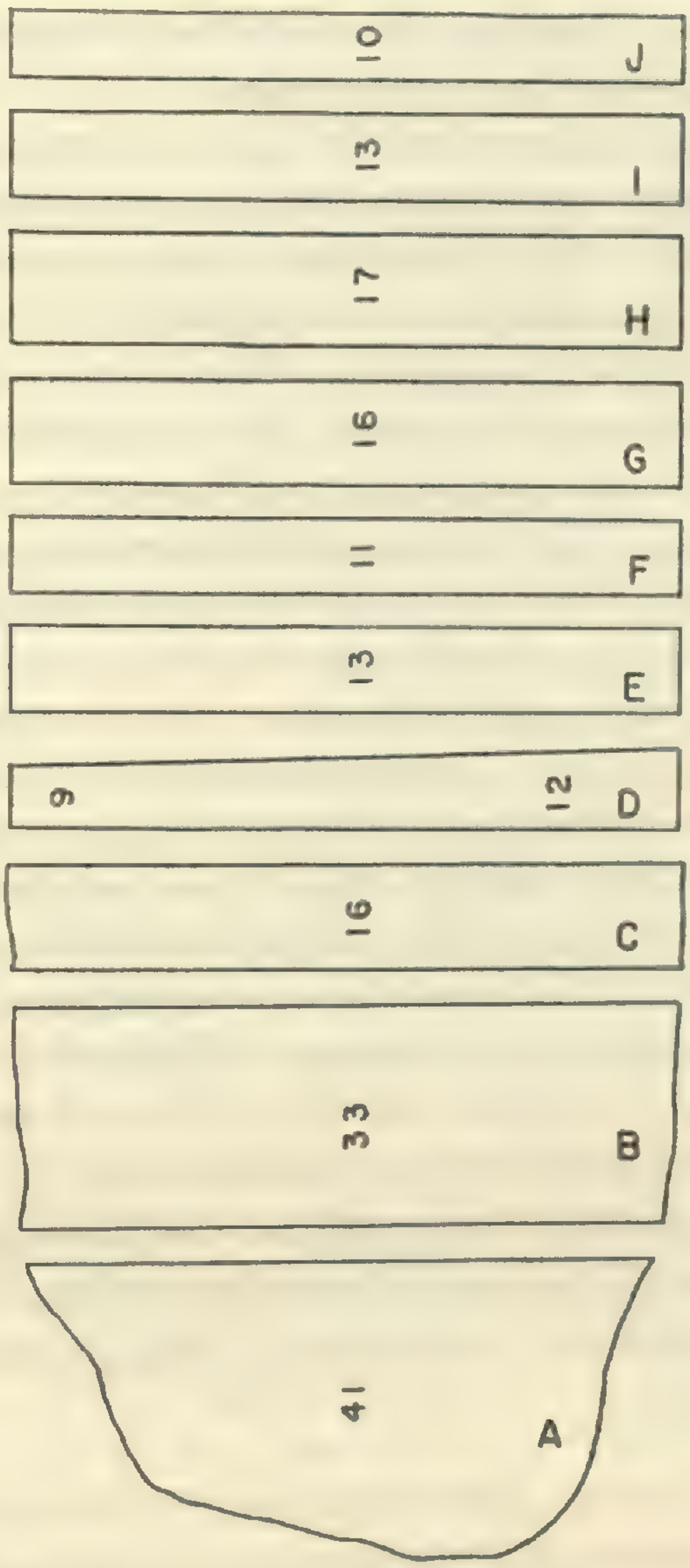
Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

MEDULLOSA DISTELICA Schopf

Another *Medullosa* specimen (No. 688) from the West Mineral, Kans., locality appears to be referable to this two-stelar species described by Schopf (1939) from the No. 6 coal of Illinois. It is basically a two-stelar specimen but presents certain variations which seem significant in furthering our knowledge of what may be considered to be specific boundaries in the genus.



Text-fig. 3. Profile of coal ball No. 688 containing specimen of *Medullosa distelica*. Numbers indicate thickness of the blocks in centimeters.



Text-fig. 4. Profile of coal ball No. 819 containing specimen of *Medullosa heterostelica*. Numbers indicate thickness of blocks in millimeters.

It has been possible to follow the stem through a distance of approximately 10 cm. (text-fig. 3). The stelar system and the enclosing periderm are quite well preserved, but the cortical tissues have been distorted and a considerable amount lost. In block *A* the stem is composed of two strongly endocentric steles (fig. 4). In the stem's course through the lower part of block *B* a small stele separates from one of the original two, producing a three-stelar system. After another 4 cm. the two-stelar phase is resumed, but since the preservation is poor beyond this point it has not been possible to determine whether any other changes take place.

The two principal steles measure about 18 × 6 mm. and 14 × 5 mm.; taking into account the obvious crushing, they measured approximately 18 × 8 mm. and

14 × 7 mm. in life. The small branch stele is nearly round in cross-section, measuring 5 mm. in diameter.

The primary body of each stele consists of scattered groups of tracheids and abundant parenchyma (fig. 9). A similar ratio occurs in *Medullosa endocentrica* (Baxter, 1949), presenting a rather striking contrast to certain other species such as M. *primaeva* and M. *thompsonii.*

In the type specimen of M. *distelica* (Schopf, 1939) the preservation of the primary wood was poor. The position of the protoxylem elements was not determined; and even in the well-preserved primary wood of the present specimen it is not possible to locate with certainty any regular position of protoxylem elements, so few and scattered are the primary tracheids.

The organization of secretory canals and fiber strands in the outer cortex or rind seems quite distinctive. An especially well-preserved portion of a petiole is shown in fig. 17, although essentially the same relationship may be observed in the stem. Starting at the outside it may be noted (fig. 10) that the secretory canals reach to within less than 1 mm. of the periphery. Here they are minute, the smallest being about 0.1 mm. in diameter, and are closely associated with the fiber strands. The canals increase in diameter toward the inside, reaching a maximum of approximately 2.5 mm. Within the rind proper the canals are conspicuously enclosed on three sides by a fibrous sheath. Only the outermost canals have an inconspicuous sheath or none at all.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

MEDULLOSA HETEROSTELICA Stewart & Delevoryas

Shortly after Stewart and Delevoryas (1952) described M. *heterostelica* from West Mineral, Kans., the present writers collected from the same locality a coal ball (No. 819) containing a stem which displays strikingly similar gross morphology. The stem has two steles which divide into more than fourteen, presumably in the nodal region. It differs from the type specimen, however, in two ways:

1. The two original steles in No. 819 measure about 16 mm. in diameter (xylem only) and are radially symmetrical with reference to both primary and secondary wood. The steles of the type specimen measure 5 × 8 mm., being less than one-half the diameter of those in our specimen.

2. The over-all size and form comparison is also reflected in the primary wood. The ratio of tracheids and parenchyma in the primary wood of the two seems to be comparable; but in No. 819 the size of the tracheids is conspicuously greater, and the primary body is nearly circular, whereas that of the type specimen is elongate.

A wholly satisfactory comparison of the two is impossible since the cortical tissues and leaf bases of our specimen are not preserved. It is, therefore, only on

the characters cited above that a decision as to specific identity can be made.

The chief point of interest that the specimen presents is the remarkable multiplication of steles in what we assume is the nodal region. This is in notable contrast to the stelar anatomy of any other species of *Medullosa*, and it is of course important to determine whether it is a specific character in itself. The evidence to date indicates that some species did not follow this pattern, whereas with others (based on short or fragmentary specimens) we cannot be certain.

A profile of the coal ball is shown in text-fig. 4. The stem appears about midway through block *A* and runs through the remainder of the specimen, totaling about 15 cm. As an introduction to a more detailed description it may be noted first that the stelar system consists of two steles, each of which gives off numerous branches which continue to divide and fuse. Although there is some interfusion between these two "systems," they tend to remain distinct. Beginning about midway through block *A* two steles make their appearance (fig. 11). They measure approximately 16 mm. in diameter, are essentially circular in cross-section, and have uniformly developed secondary wood. The primary wood consists of tracheids with a few parenchyma cells and measures about 2.5 mm. in diameter. Other than fragmentary pieces of the cortex, no tissues are preserved outside the xylem. These two steles are arbitrarily designated *A* and *B* for the purpose of identification in this description.

The two steles remain unchanged until about midway through block *D*, at which point (text fig. 5-2) a stele departs from *A*. Another small separate stele may also be noted here; this and several others were observed in a peripheral position and were not traced to an attachment with *A* or *B*; lack of attachment is due apparently to faulty preservation. At a slightly higher level, midway through block *E*, several branch steles are now evident (text fig. 5-3). These represent additional branches from *A* and *B* and the divisions of branches themselves.

It will be noted from the text figures as well as the photographs that many of the steles are only partly preserved. Most notable is the gradual loss of stele *A*. The preservation is poor at the level shown in text-fig. 5-3; at the level of text-fig. 5-5 only half of it is present, and by the time block *J* is reached (text-fig. 5-7) it has disappeared. Stele *B* retains essentially the same size and form through the specimen and is at all times dominant in relation to its branches; it seems likely, judging from the portion of it that is preserved, that stele *A* followed the same pattern. The preservation in block *H* is very poor, and little of significance remains beyond block *J*.

For the most part, the branch steles shown on the left side of the text-figures come from stele *A* and those on the right side from stele *B*. A union of the two "systems," however, is evident in text-fig. 5-6 in the form of the elongate stele in the upper part of the figure.

The maximum number of steles present at any one point can be determined only approximately, because of faulty preservation and in part because of the prolific anastomosing nature of the system. For example, in text-fig. 5-6 a more

Text-fig. 5. *Medullosa heterostelica.* Transverse diagrams of specimen No. 819 showing changes in the stelar form through blocks C–J (see text-fig. 4). Several of the poorly preserved steles are omitted. 1, C-t2; 2, D-t17; 3, E-t14; 4, F-t16; 5, F-t9; 6, G-t1; 7, J-t1.

or less 7-shaped stele may be noted encompassing the right side of the figure, whereas 16 mm. above (text-fig. 5-7) this has divided into five or six steles. At the latter point, which may be taken as representative of the more highly divided part of the stem, there are about fourteen whole or fragmentary steles.

So poorly is the stem preserved beyond block *J* that we are unable to determine whether or not it passes back into the two-stelar phase as reported for the type specimen. The lack of cortical tissues and petiole bases also makes it impossible to determine which steles contribute directly or indirectly to the petiole trace system.

The only previously described *Medullosa* specimen with which this may be compared closely is *M. heterostelica.* As stated above, it differs most notably in size, the two central steles being twice as great in diameter as those of the type specimen. Assuming that the multiple stelar condition in our specimen is also a nodal region, the size contrast is comparable here. This region is described as being approximately 5.5 cm. long in the type specimen (Stewart and Delevoryas, 1952, p. 508, figs. 5 and 12). In our specimen the multiple-stelar phase starts in block *D* and runs through *J*, a distance of 9.3 cm., and undoubtedly ran for several centimeters more if indeed it did again assume the two-stelar phase.

Aside from the size there is nothing on which to base a specific difference, and for that reason our specimen is assigned to *M. heterostelica.*

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

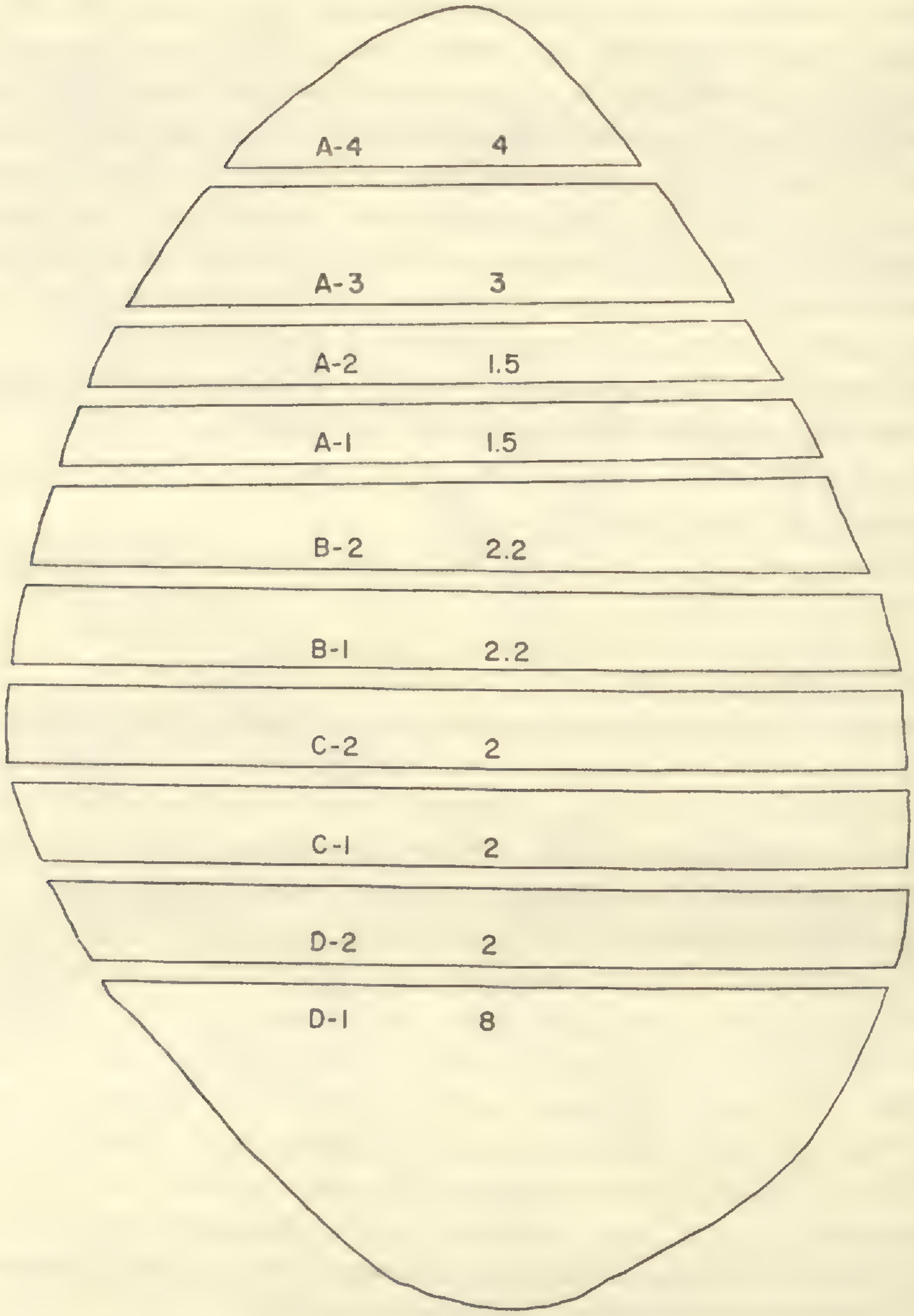
Medullosa **grandis** sp. nov.

The most unique medullosan specimen that we have acquired in recent years is No. 718 from the West Mineral, Kans. locality. It is especially interesting by virtue of its large size and by its numerous steles which anastomose freely and present much anatomical variation. With the exception of *Medullosa noei* it is much larger than any of the previously reported Carboniferous species.

The specimen composes the major portion of a coal ball about 30 cm. long and 28 × 12 cm. in its largest transverse dimensions. The coal ball tapers to a very blunt point at the *A* end (text-fig. 6) and the stem decreases correspondingly in size; that is, the decrease is normal and not due simply to loss of part of the stelar system. This small end is also heavily pyritized and less well preserved than the rest of the specimen. The other end is represented by a broken surface. If, as seems likely, this specimen constitutes the apical portion of a stem, then it clearly represents a tree of some magnitude; and if the stem continued to increase in diameter for an appreciable distance at the rate shown in our fragment it must have soon attained the dimensions of a large forest tree.

In order to present a clear picture of the complex organization of the stelar system a restoration of the major portion of it is shown in text-fig. 7. This is accompanied, in text-fig. 8, with diagrams of the system at the four points indicated. All the numerous smaller steles that show in text-fig. 8 are not included in the restoration (text-fig. 7). Text-fig. 6 is a profile of the coal ball, which may be referred to for the position of the text and plate figures.

A casual glance at the text-figures reveals considerable variation in the size and shape of the steles as well as the relative amount of primary wood that is present. A striking feature is the great variation in the structure of the secondary wood itself, in which the different ratios of parenchyma and tracheids present distinctly atypical steles. It is of course likely that many of the smaller strands



Text-fig. 6. Profile of coal ball No. 718 containing the specimen of *M. grandis*. Numbers in the right column indicate thickness in centimeters.

contribute to the vascular supply of the petioles. Of necessity we are therefore using the term "stele" to include all the vascular strands with secondary wood (secondary phloem is present but poorly preserved).

In tracing the over-all pattern of the stelar anatomy it is significant to note that it is composed of two fairly distinct systems, thus following in a general way the type of organization described for *Medullosa heterostelica*. Stelar branching and fusion take place so rapidly that the system presents an intricate anastomosing network. The block is so large that it did not seem practicable to run a complete

Text-fig. 7. A restoration of the stelar system of *Medullosa grandis*.

series of sections through the specimen. Text-fig. 7 presents, therefore, a slightly less complex picture than that actually represented by the number of steles involved and the branching pattern.

The numbers assigned to the individual steles in text-fig. 8 *A–D* are arbitrary and are intended to facilitate following the steles through the portion of the stem that is represented. It seems somewhat simpler to start with the smaller end, presumably the apex of the stem. We may first follow the course of steles 1, 2, and 3 from *A* to *B*, where steles 1 and 2 have fused and stele 3 is evidently preparing to divide. In *C* the three steles are shown fused into a single irregular-shaped stele. Finally in *D* this has now divided into four distinct steles. These fusions and divisions take place through a distance of approximately 10 cm.

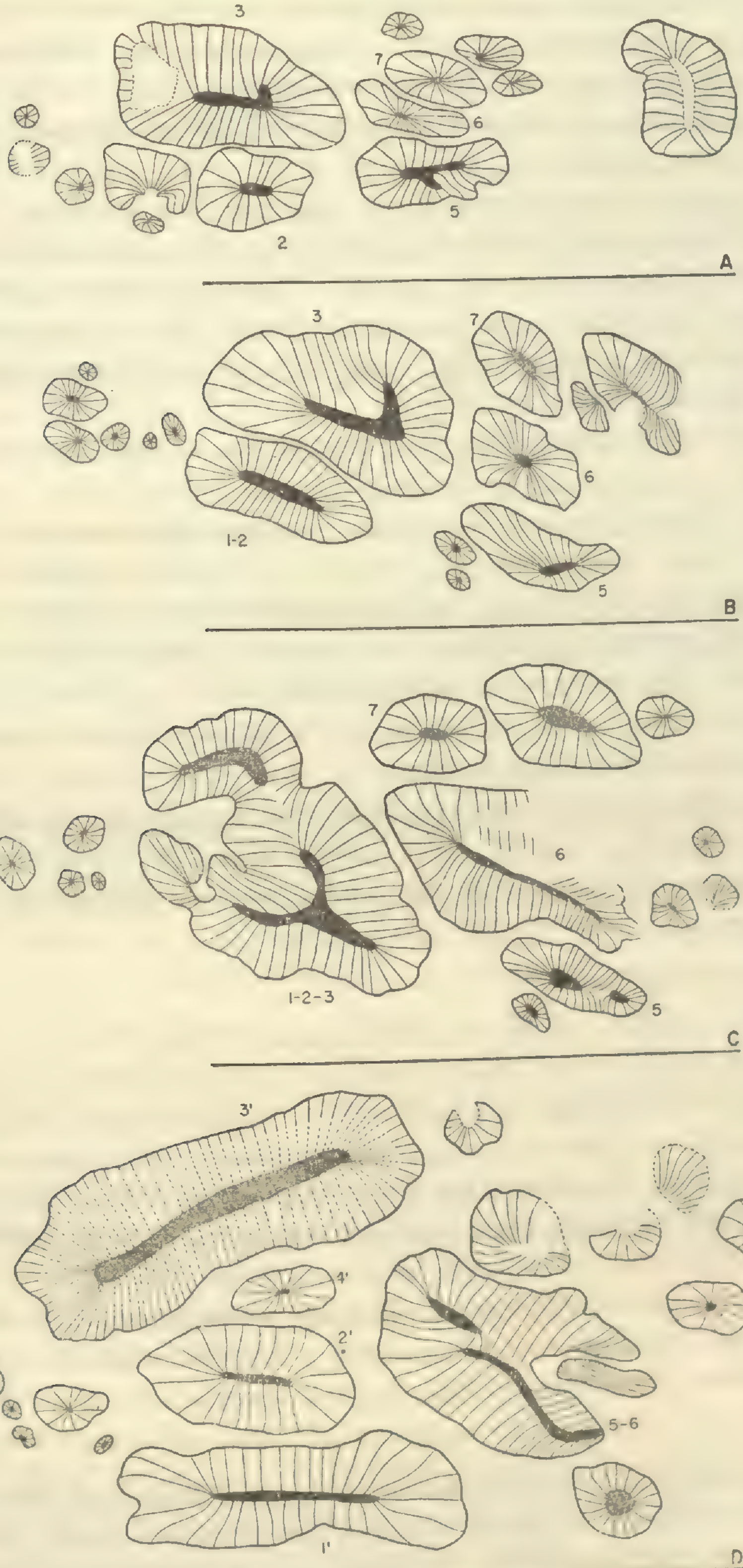
Returning to text-fig. 8-*A* we may now trace through the second "system" of steles, represented here by numbers 5, 6, 7; these also increase markedly in size in passing through *B* to *C*. Because of faulty preservation it was not possible to interpret precisely the changes that ensue below this point. At least one branch stele departs from number 5, and in *D* steles 5 and 6 are fused to form a very irregular-shaped wood mass. There can be little doubt that the numerous smaller steles shown to the right are a part of this stelar "system," but they have not been traced in actual connection.

In addition to the more conspicuous steles considered above there are numerous smaller ones all of which display a remarkable range of variation in their organization. Certain of these features may now be considered.

Figure 13, which represents a single stele from the cross-section shown in fig. 1, may be taken as typical of the organization of the larger "normal" vascular elements of the stem. The stele is slightly crushed, although it is evident that there was no great abundance of primary wood. In fig. 14 is illustrated a portion of another stele of generally comparable dimensions. It is evident here that the primary wood is composed chiefly of tracheids with little admixed parenchyma. There is nothing exceptional about the organization of the secondary wood of the stele shown in fig. 13. The pitting in the radial walls of the tracheids is typically pteridospermous, and the rays are rather narrow and of great height.

Several of the larger steles compare with the one described above, but others vary much in their course through the stem with respect to the relative abundance of parenchyma and tracheids, and this difference may be noted in both primary and secondary wood.

Figure 16 shows a portion of the large stele at the upper right of fig. 1. The central region of this stele is occupied by parenchyma exclusively, whereas the immediately surrounding secondary tissue consists chiefly of parenchyma with a few radially aligned rows of tracheids, a feature that is common in the secondary xylem of some of the large Permian Medullosas. Toward the periphery of the stele the organization compares closely with that observed in the stele shown in fig. 13. It should be kept in mind here that the stele shown in fig. 16 is directly connected with the "normal" stele shown in fig. 13.



Text-fig. 8. *Medullosa grandis.* Transverse diagrams of specimen 718 showing changes in the stelar form through blocks A–C (See text-fig. 6). A, A-t2; B, B2-t1; C, B1-t1; D, C-t1.

Another predominantly parenchymatous stele is illustrated in fig. 15. Here there is a large pith composed chiefly of parenchyma but with some groups of tracheids scattered through it. The tracheid-parenchyma cell ratio in the secondary wood is variable, as is indicated in the figure. A small branch stele preparing to depart is shown at *B*.

Most of the extra-stelar tissues of the specimen have been lost, but the fragments of the characteristic medullosan internal periderm suggest the enclosure of the stelar system here as in other species. There is a rather poorly preserved groundwork of parenchyma, and scattered through this are numerous secretory canals, each enclosed by a "periderm" ring. Several small traces are present, also enclosed in the same tissue (fig. 8).

There is no evidence suggesting that any portion of this specimen represents a nodal region.

Diagnosis: Stem large, greatest known traverse dimensions of the stelar system 12 × 28 cm. Steles numerous (18–20), extremely variable in size (up to 6 cm. in diameter), shape, and xylem-parenchyma ratio. Steles anastomosing frequently, but generally arranged in two systems, one somewhat more complex than the other. Extra-stelar organization unknown.

Locality: Strip mine of the Pittsburgh & Midway Coal Co., approximately four miles south of West Mineral, Kans.

Horizon: Fleming Coal, Cherokee shale, Des Moines group, middle Pennsylvanian.

Type specimen is deposited in the Paleozoic plant collections of the U. S. National Museum.

Medullosa noei Steidtmann

Our recent coal-ball collections from southern Illinois include two specimens of the large tri-stelar *M. noei* (Steidtmann, 1937, 1944). They are approximately 43 cm. and 30 cm. long; although this is intended only as a preliminary account, since the two have not been studied critically, they appear to follow the general stelar pattern described above for *M. thompsonii*. They show no evidence of the multiplicity of stelar branching and fusion found in *M. heterostelica* and *M. grandis*.

One of the specimens showing the complete stelar system is illustrated in fig. 18; the original specimen was a fragmentary one, although the concept of its stelar organization (Steidtmann, 1937, fig. A) is confirmed by our specimens.

Discussion:

Several contributors to the literature on the Medullosas have been tempted to speculate concerning the relationships of the now numerous species included in the genus. A total of no less than 44 species and varieties have been recorded to date, and since the stelar anatomy is nearly as diverse as the number of entities recorded it is understandable that paleobotanists find it intriguing to propose evolutionary lines in the group. Although the primary purpose of this paper is to present

what appear to be significant factual contributions, a few speculatory comments seem to be in order.

One point of anatomical significance is well illustrated by the assemblage of specimens discussed in this paper, namely, the contrast in the relative constancy of stelar number among certain of the better-known species.

Medullosa endocentrica Baxter may be taken as a striking example of a species in which the stelar number remains constant. The single available specimen was some 12 cm. long, a significant length considering the small diameter of the plant. In this specimen the tri-stelar form remains constant throughout its length, there being no evidence of stelar fusion, division, nodal complexities, or notable changes in shape or size of the individual steles. Based on observations of a specimen some 23 cm. long, *M. thompsonii* also displays a relatively simple stelar pattern. There is some stelar division and fusion; this, however, is not apparently related to the position of the nodes, and the number of steles varies only from two to three (text-fig. 2).

The stelar complexity of *M. grandis* and *M. heterostelica* presents, at least on casual observation, a striking contrast to the organization found in *M. endocentrica* and *M. thompsonii*. The contrast may cause one to question the inclusion of all four species within one genus. The complex stelar form of *M. grandis* and *M. heterostelica* does, however, mask an apparently basic pattern of organization. We have demonstrated that, so far as preservation allows, our specimen of *M. heterostelica* contains a two-stelar system. That is, the two "original" steles each divide profusely, but the two resultant groups of steles remain more or less distinct. In *M. grandis*, also, the stelar system appears to be organized into two groups, although we are unable to determine whether or not the specimen at our disposal represents a nodal region comparable with that of *M. heterostelica*. In view of the rather significant size of the specimen of *M. grandis*, it seems likely that the stem did not possess the two-stelar internodal simplicity of *M. heterostelica*.

One point can be stated with certainty concerning the interrelationships of the Medullosas is that we can guess, and guess only vaguely, concerning possible lines of development. The extent to which competent workers have disagreed in their concepts of racial development in the genus is indicated by comparing the phyletic chart of Baxter (1949, p. 309) with that presented by Stewart and Delevoryas (1952, p. 514). In the latter, *Sutcliffia* is assigned a basal position, whereas Baxter suggests that *Sutcliffia* represents a specialized side branch from a *Medullosa* of the *M. anglica* type. It is also significant that the discovery of *M. heterostelica* caused Stewart and Delevoryas (1952) to modify rather radically the concept presented in Stewart's earlier paper of 1951.

It is thus evident that the discovery of each new species of *Medullosa* may result in a new phyletic scheme for the genus, particularly in view of the unique specimens that have been discovered in recent years. Our feeling is that inter-

relationships within the genus are actually much more complex than has been implied by previous workers. Evidence in support of this view is contributed by the recent report of *M. olseniae* from the Permian of Texas (Roberts and Barghoorn, 1952). It is a multi-stelar stem, the steles being arranged in a peripheral group resembling *M. leuckarti* or *M. solmsi*, but subsidiary steles are reported to be lacking. It is thus difficult to "fit" it into the top of either of the two branches of the genus indicated in the chart presented by Stewart and Delevoryas.

Although we shall refrain from commenting further on the evolution of the genus as a whole, we should like to conclude with a comment on the type of anatomy presented by the *grandis-heterostelica* complex. It has been assumed by many previous workers that the Medullosas evolved from a single-steled plant of the *Heterangium* type or one in which a single stele appears dominant, as in *Sutcliffia*. Referring for the moment to the type of anatomy exhibited by *M. grandis*, there appear to be at least two possible explanations for its origin:

First, in view of the two distinct stelar "systems" represented, *Medullosa grandis* may be considered as having evolved from a *two-stelar* ancestor with stelar proliferations resulting in this type of multi-stelar stem. Further modifications of the *M. grandis* pattern may then have resulted in the diverse types found in the Permian. Then, unless we assume a *phyletic return* to the two-stelar form, *M. grandis* may be considered as an advanced species having evolved from the *anglica-thompsonii-distelica*-etc. group. Stratigraphic relations are not very helpful here. The exact position of *M. grandis* in relation to the species cited above is not known, but it seems likely that *M. anglica* is of earlier origin, while *M. thompsonii* and *M. distelica* are of later origin (see Andrews, 1951, p. 433).

Second is the possibility that *M. grandis* is a distinctly *primitive Medullosa* in which we may see the beginnings of dominance being assumed by a few steles. In this case *M. heterostelica* may represent a species in which the multi-stelar phase is confined to the nodal region and in turn the two- to three-stelar species have evolved (as suggested by Stewart and Delevoryas) by the complete loss of the multi-stelar phase. This suggestion next requires some tentative explanation concerning the origin of *M. grandis*, and it is at this point that we would diverge most radically from previous views.

In recent years several poly-stelic plants have been reported from Devonian and lowermost Carboniferous horizons such as *Xenocladia* (Arnold, 1952), *Pietzschia* (Gothan, 1927; and Read and Campbell, 1939), *Steloxylon* (Solms-Laubach, 1896, and Read and Campbell, 1939), and *Cladoxylon* (Bertrand, 1935). It is not implied that *M. grandis* may be traced directly to any of these plants, but it is suggested that such a stem *type* may represent a medullosan ancestor.

Acknowledgement:

This study has been aided in large part by a grant from the Permanent Science Fund of The American Academy of Arts and Sciences. A portion of the work was also carried out during my tenure, at Harvard University, as a Fellow of the John Simon Guggenheim Memorial Foundation. I am sincerely grateful to these several institutions.—H.N.A.

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Explanation of Plate

PLATE 16

Fig. 1. *Medullosa grandis* Andrews & Mamay. Transverse section, peel 718-C-tl. Natural size.

I.

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

EXPLANATION OF PLATE

PLATE 17

Medullosa thompsonii Andrews

Fig. 2. Transverse section of stelar system of specimen No. 721. Peel 721-B-b2. × 14.

Fig. 3. Transverse section of a single stele of specimen No. 713. Peel 713-D2-t4. × 8.

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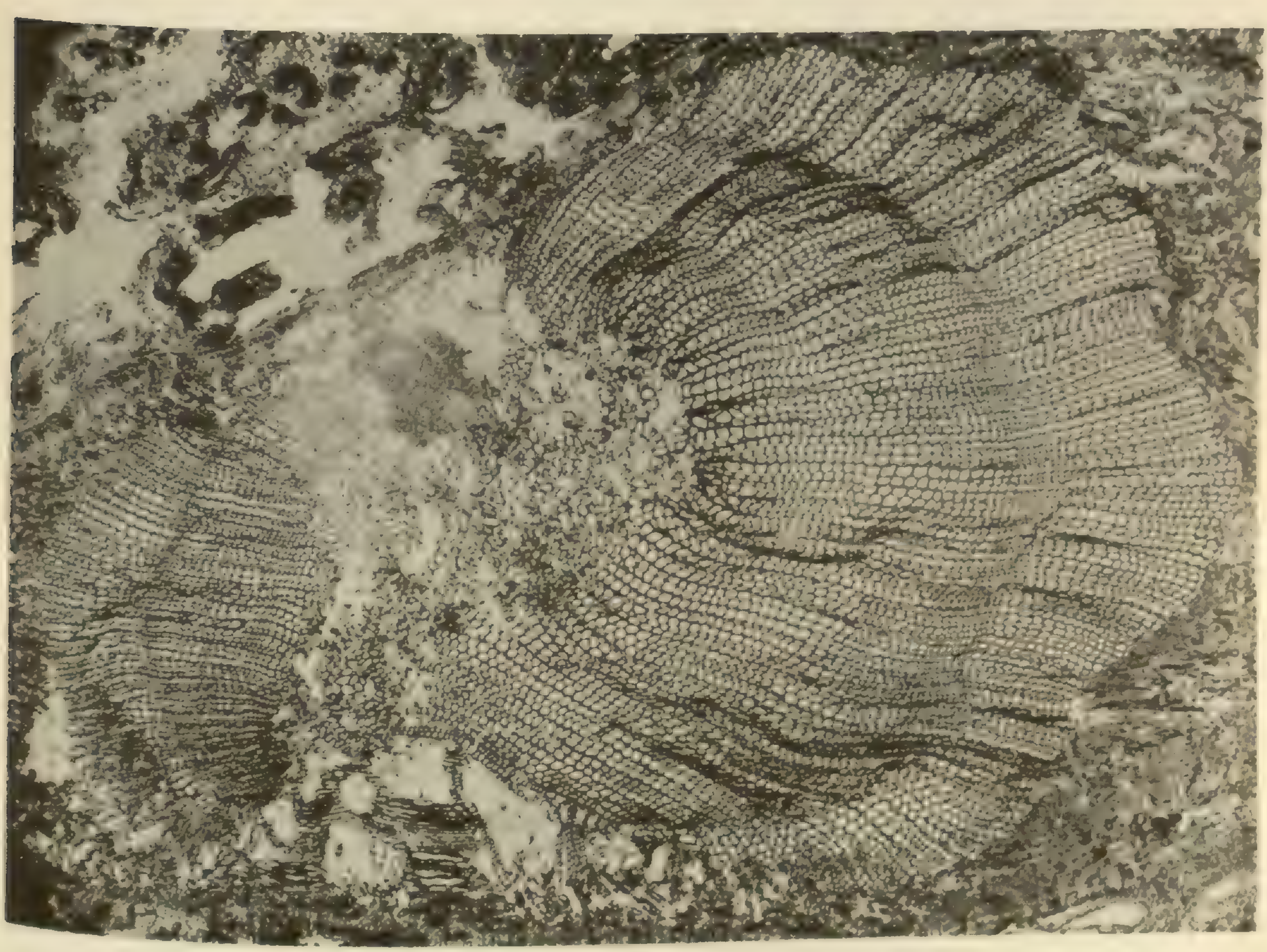

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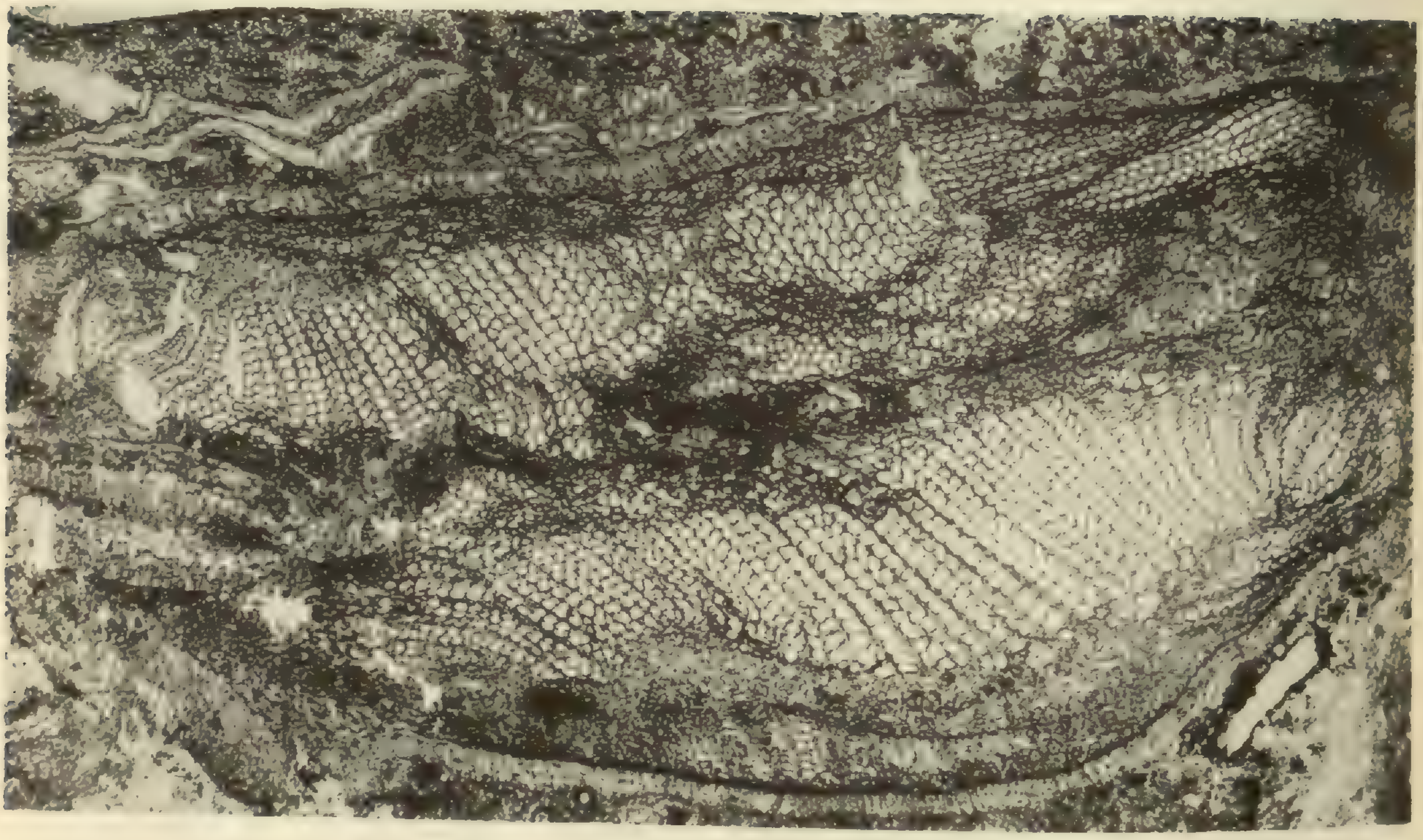

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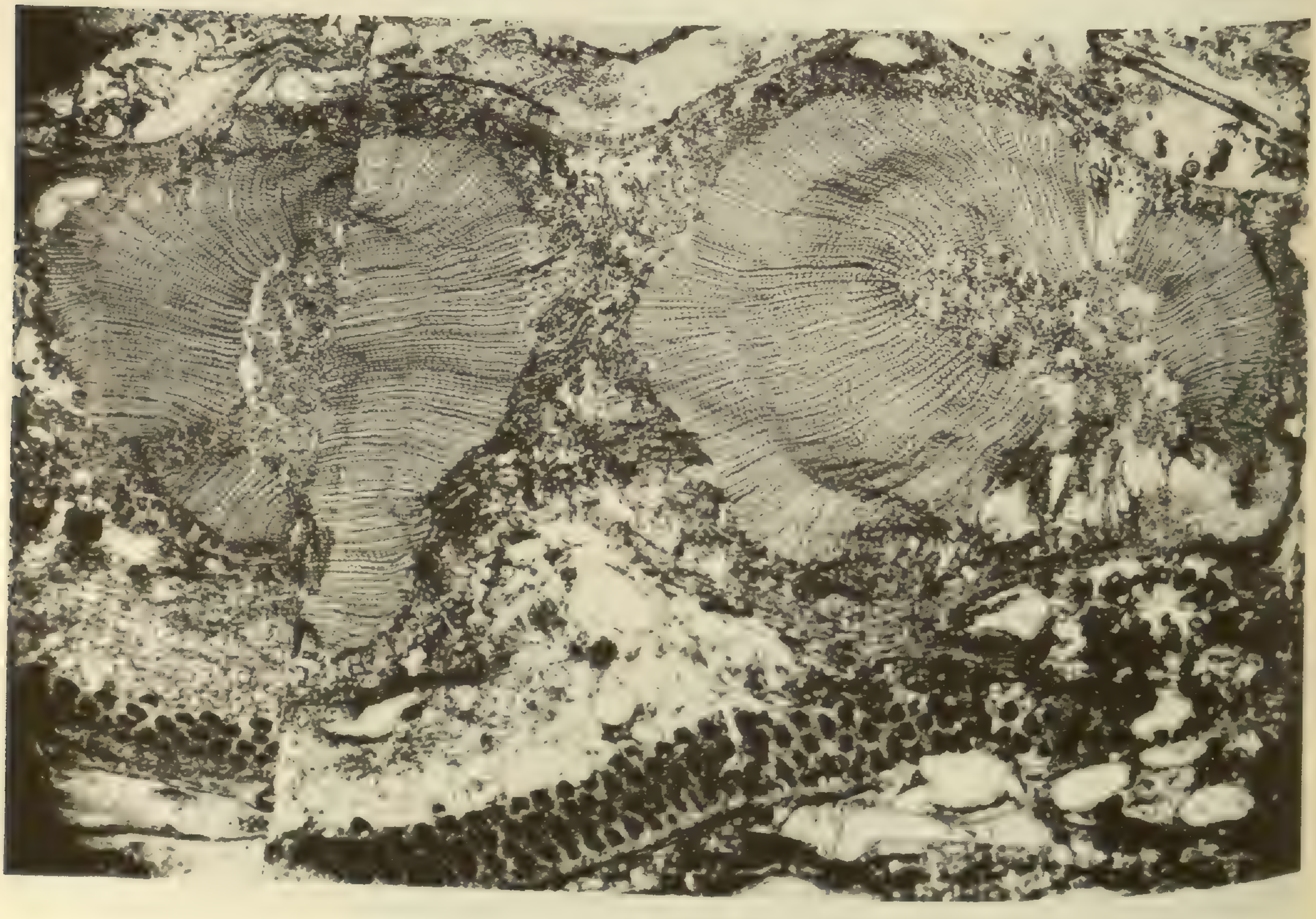

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ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 18

Fig. 4. *Medullosa distelica* Schopf. Transverse section of stelar system of specimen No. 688. Peel 688-A-t13. × 15.

Fig. 5. *Medullosa thompsonii* Andrews. Transverse section of specimen No. 713 showing two-stelar phase. Peels 713-D2-b3 and 713-D1-b3. × 4.

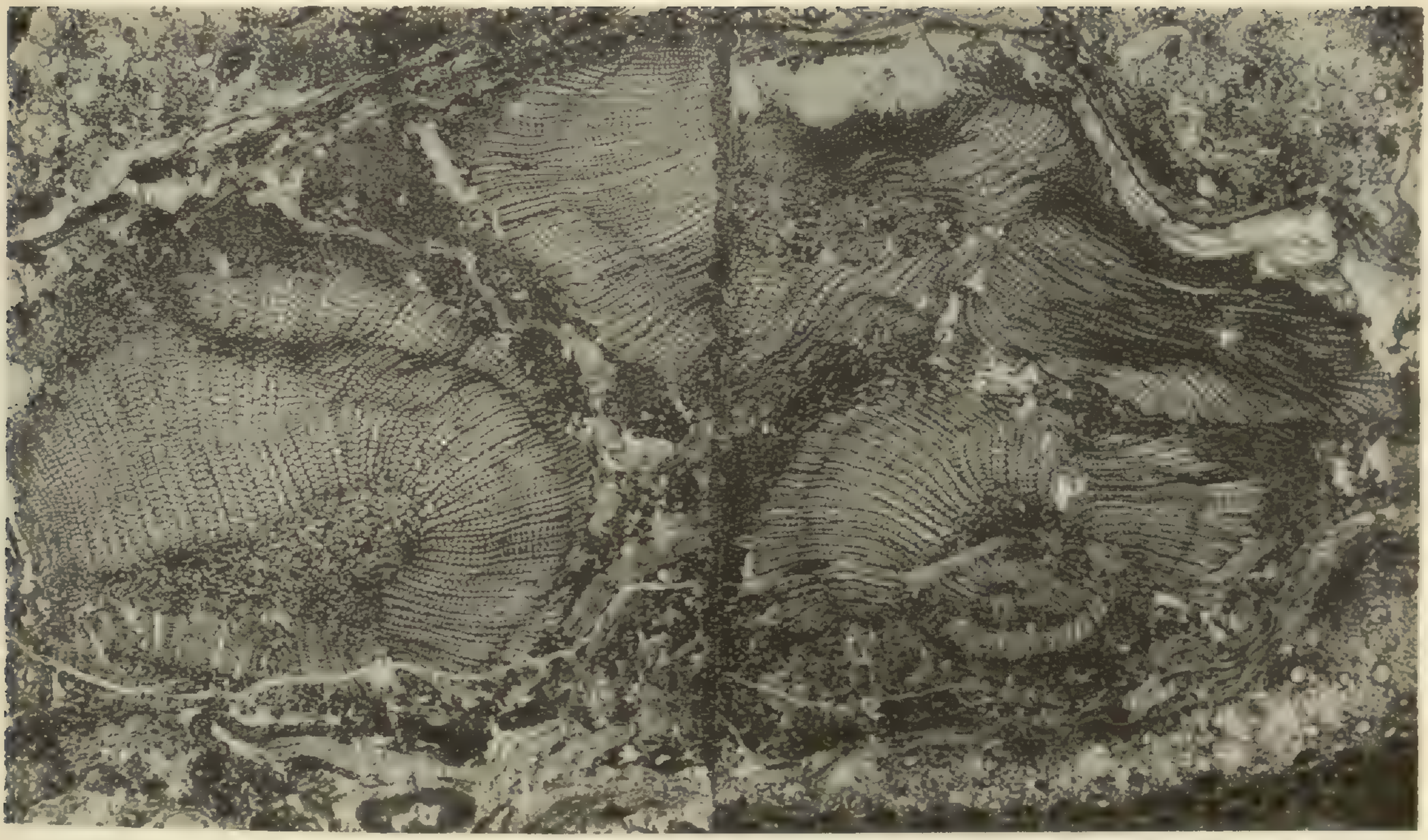
Explanation of Plate

PLATE 19

Medullosa thompsonii Andrews. Transverse sections of stelar system.

Fig. 6. Peels 713-A1-1,b2 and 713-A2-1,b2. × 4.

Fig. 7. Peels 713-B1-b7 and 713-B2-b8. × 4.



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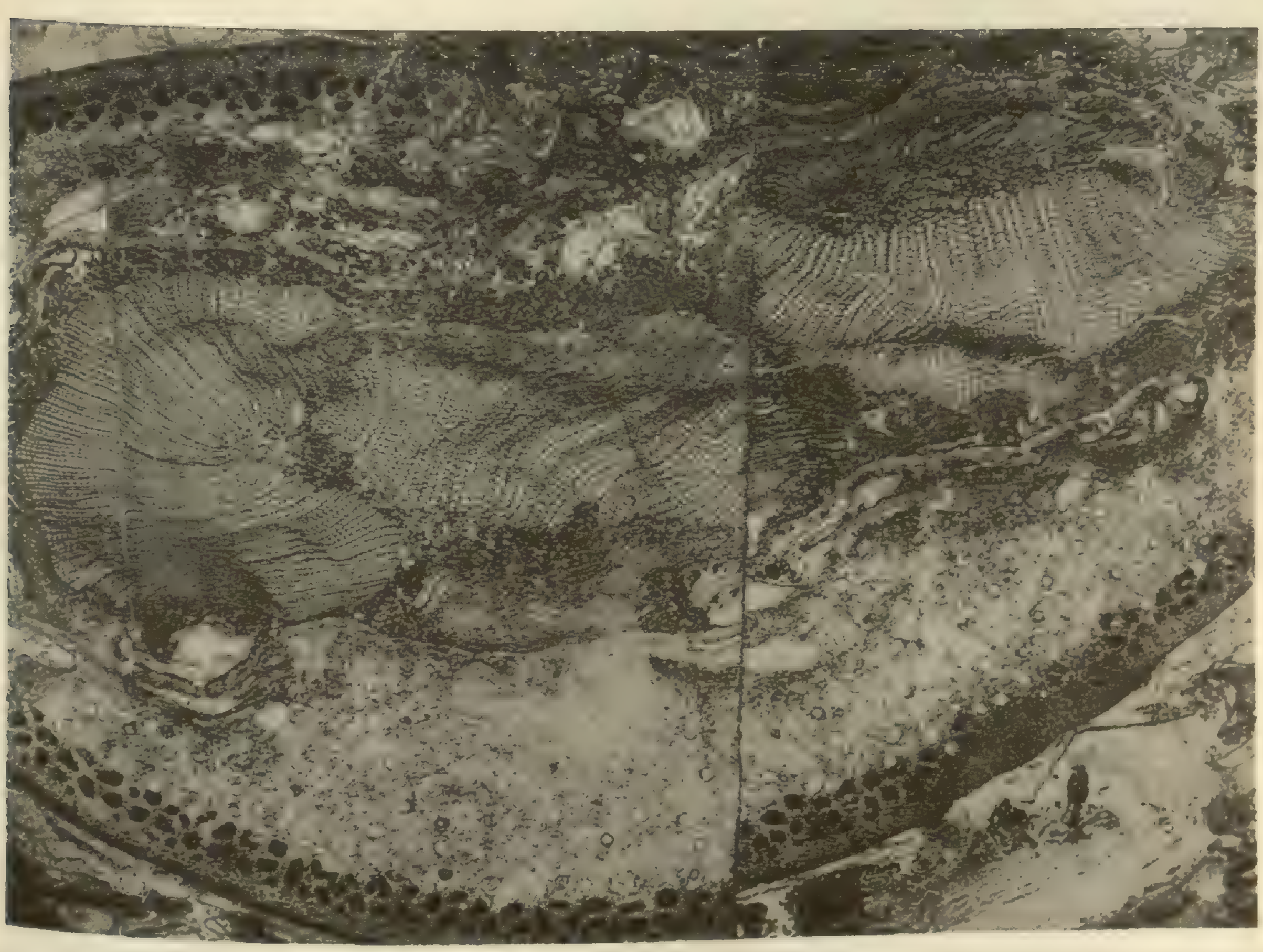

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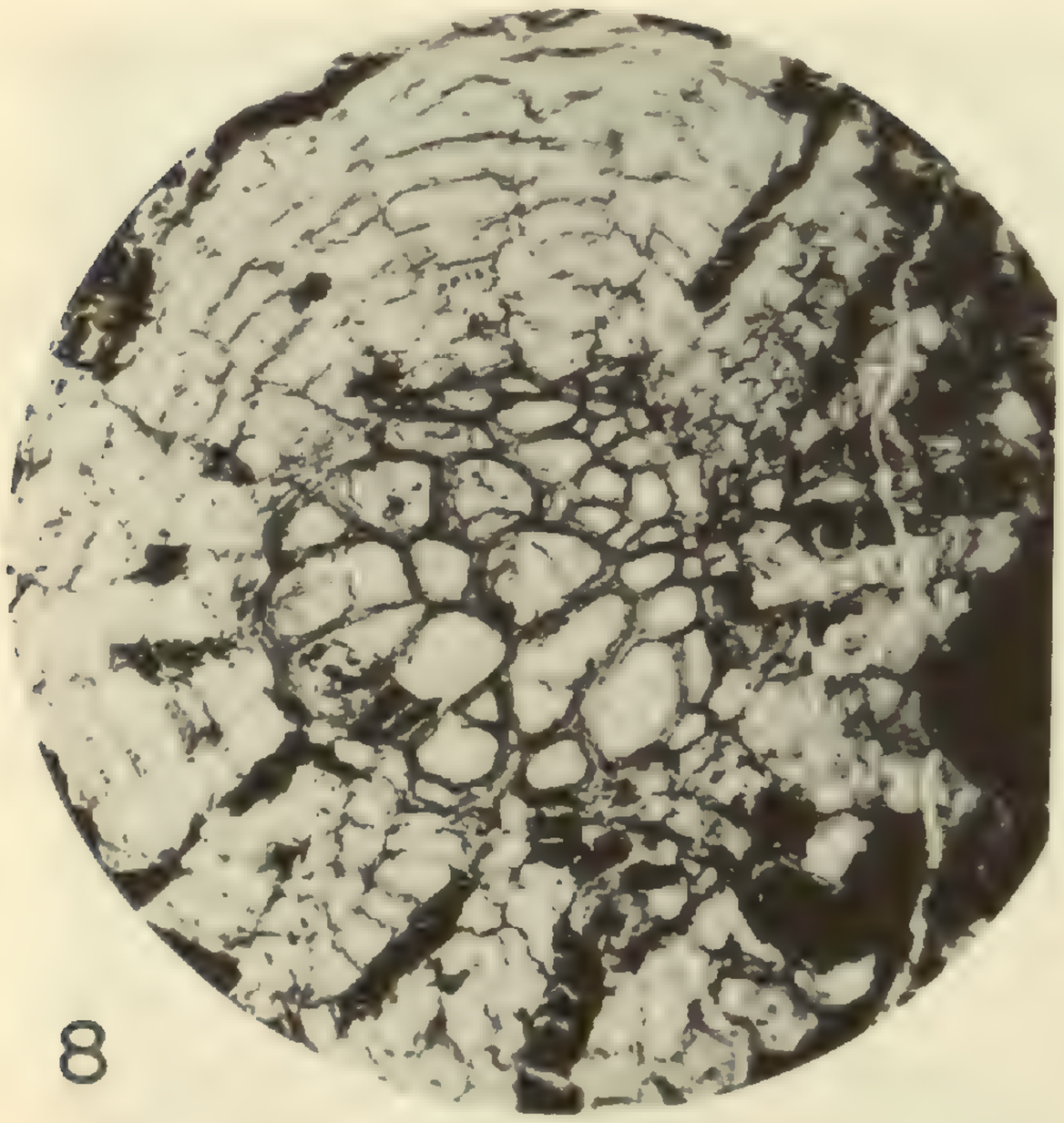
ANDREWS AND MAMAY — AMERICAN MEDULLOSAS



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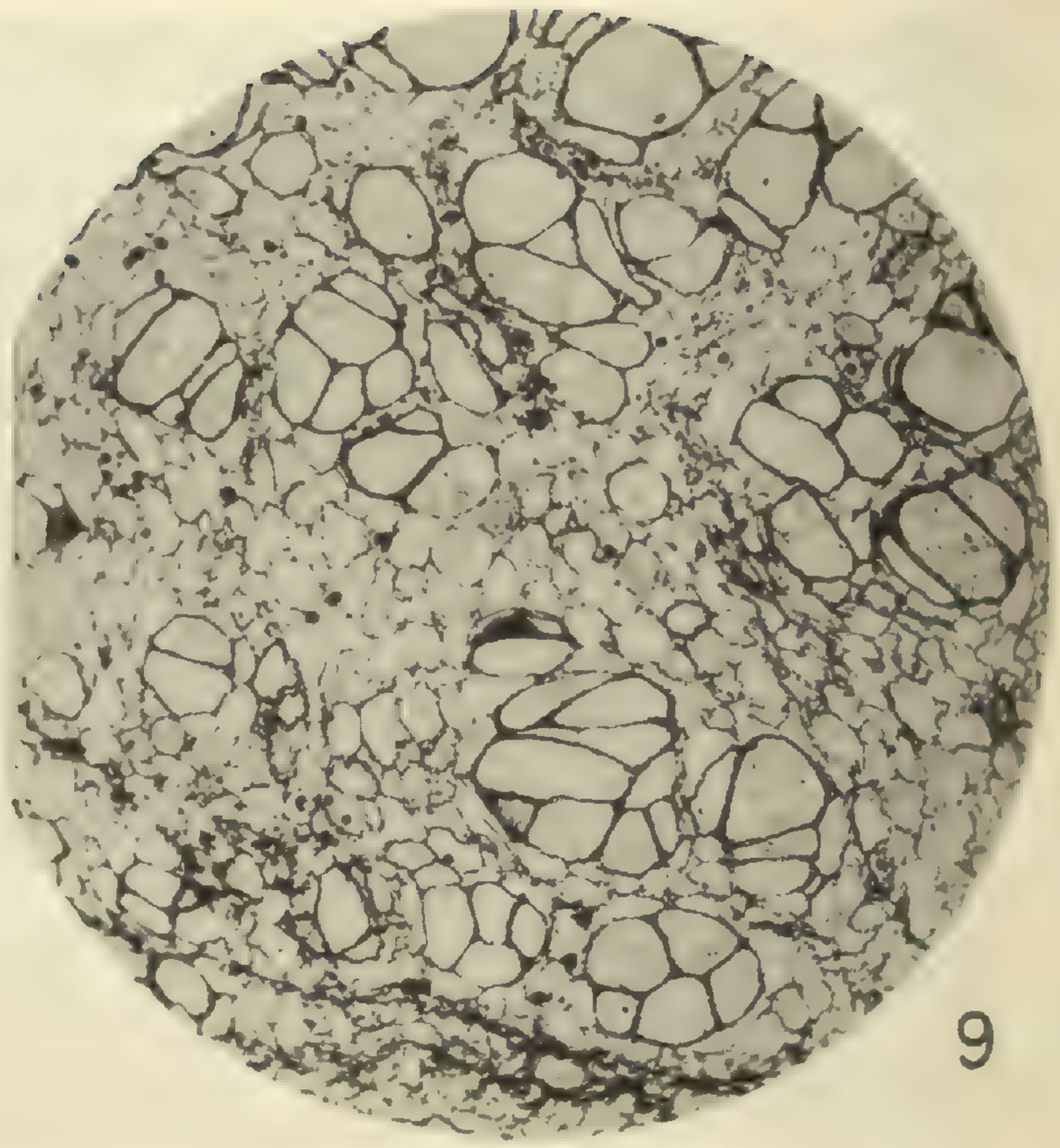

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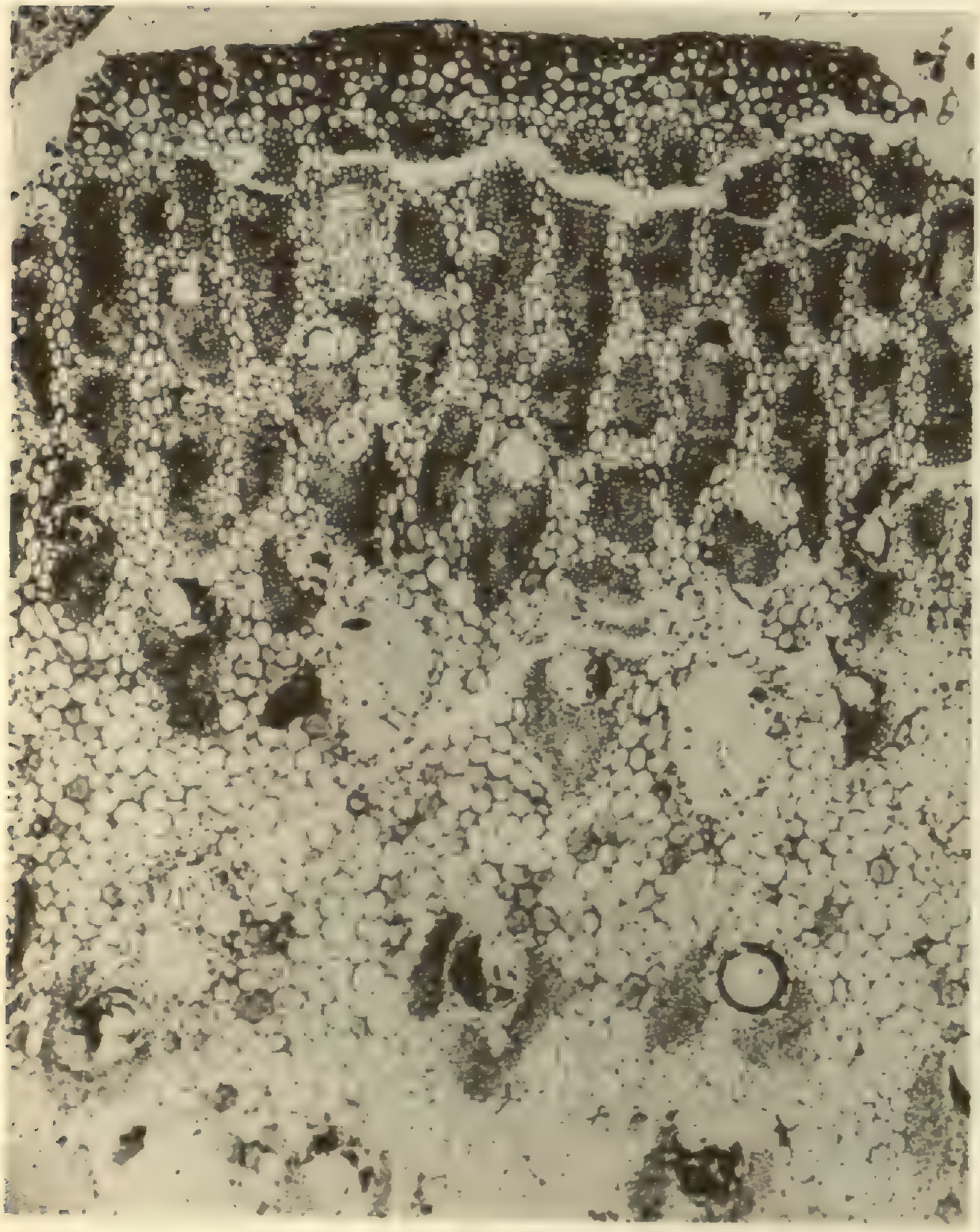

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ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 20

Fig. 8. *Medullosa grandis.* Transverse section of a small vascular strand, presumably a leaf trace, surrounded by "periderm." Peel 718-B1-t1. × 55.

Fig. 9. *Medullosa distelica.* Transverse section of primary wood. Peel 688-C-b2. × 60.

Fig. 10. *Medullosa distelica.* Transverse section of the outer cortex of the petiole. Peel 688-B-t13. × 25.

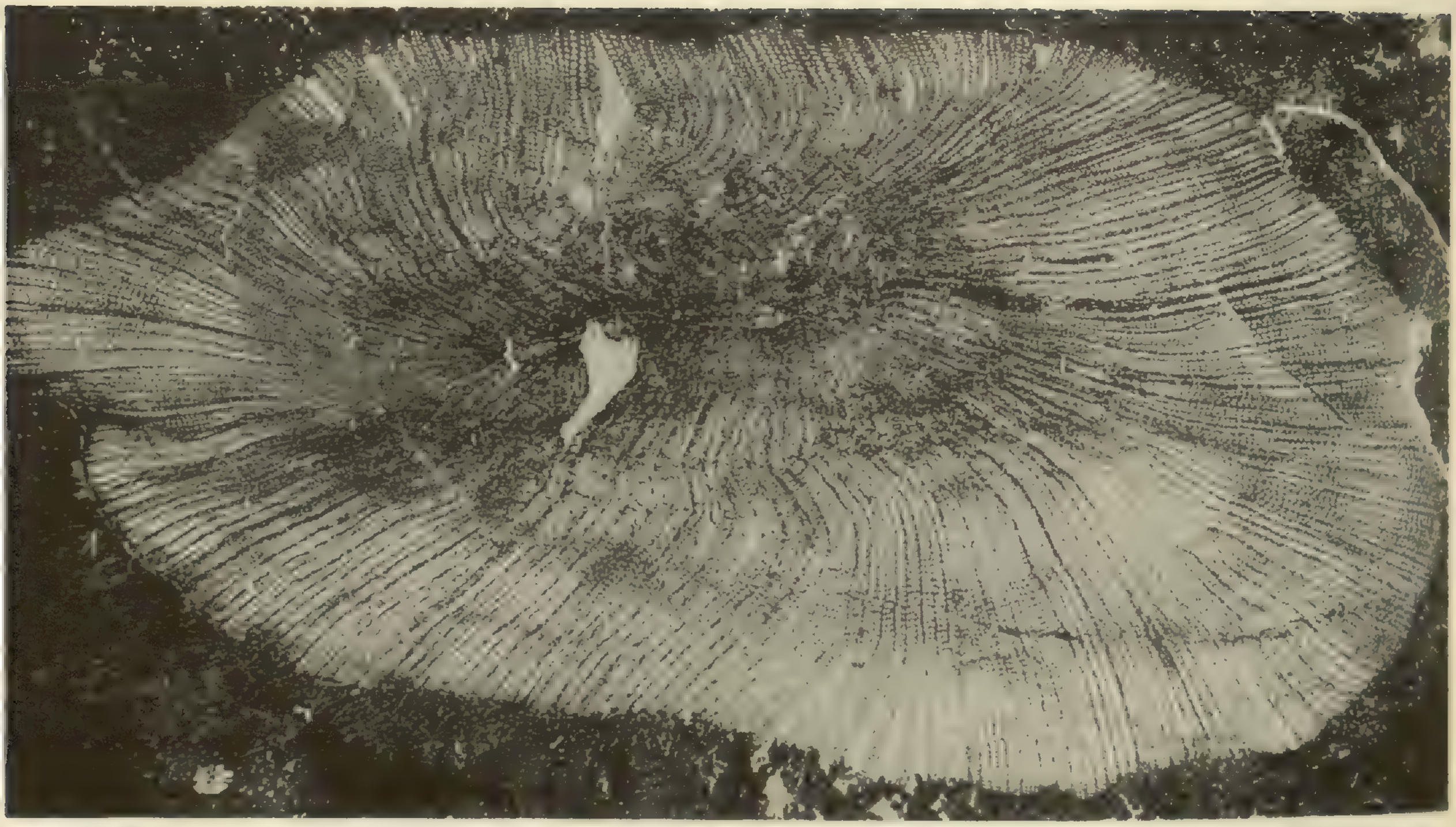
Fig. 11. *Medullosa heterostelica* Stewart and Delevoryas. Transverse section showing the two-stelar phase. Peel 819-B-t3. × 2.4.

EXPLANATION OF PLATE

PLATE 21

Fig. 12. *Medullosa heterostelica.* Transverse section of the stem showing the multistelar phase. Peel 819-G-t3. × 3.

ANDREWS AND MAMAY — AMERICAN MEDULLOSAS



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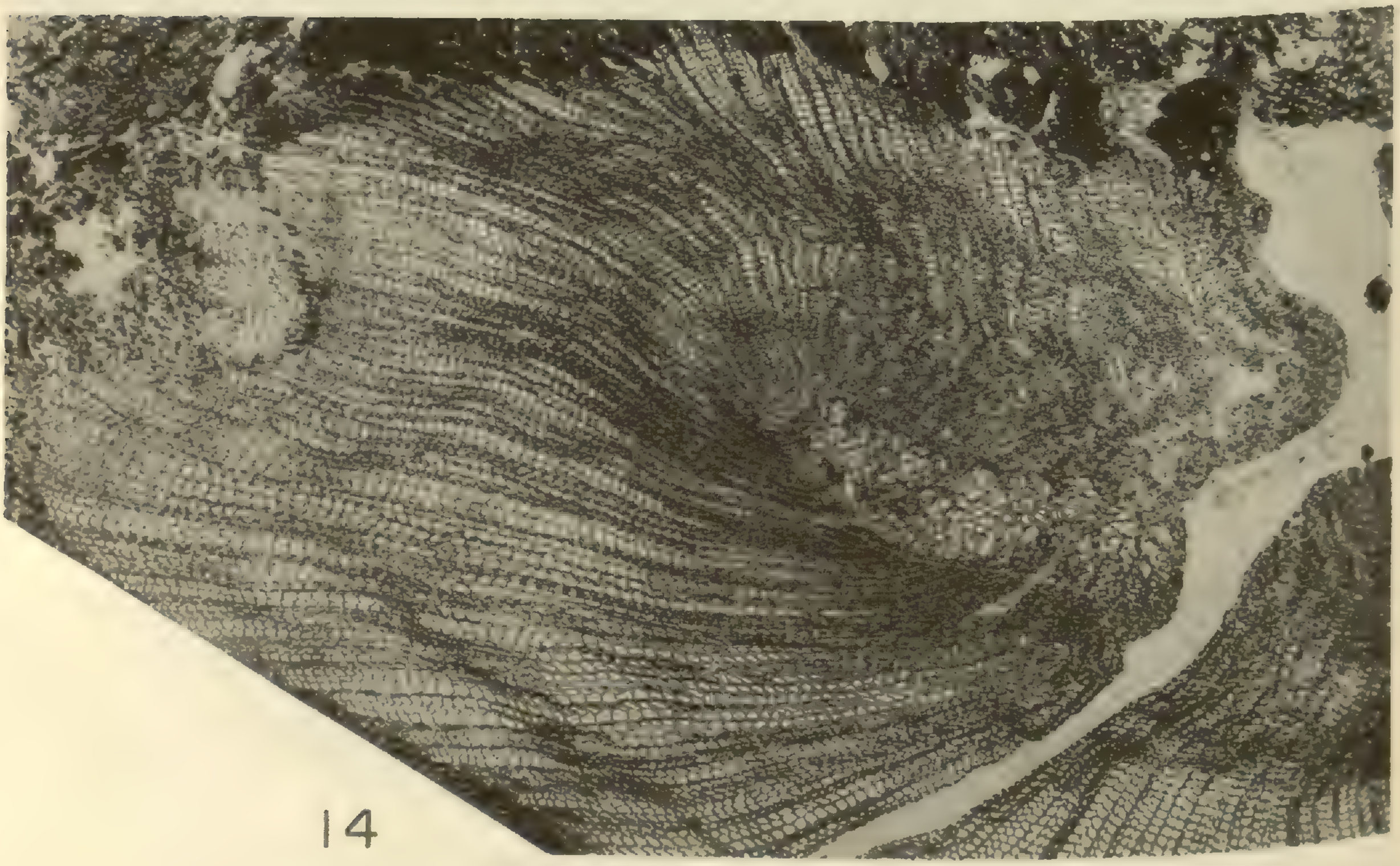

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ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 22

Medullosa grandis

Fig. 13. A single stele. Peel 718-C-t2. × 3.

Fig. 14. Portion of a single stele showing primary wood. Peel 718-B2-t1. × 6.5.

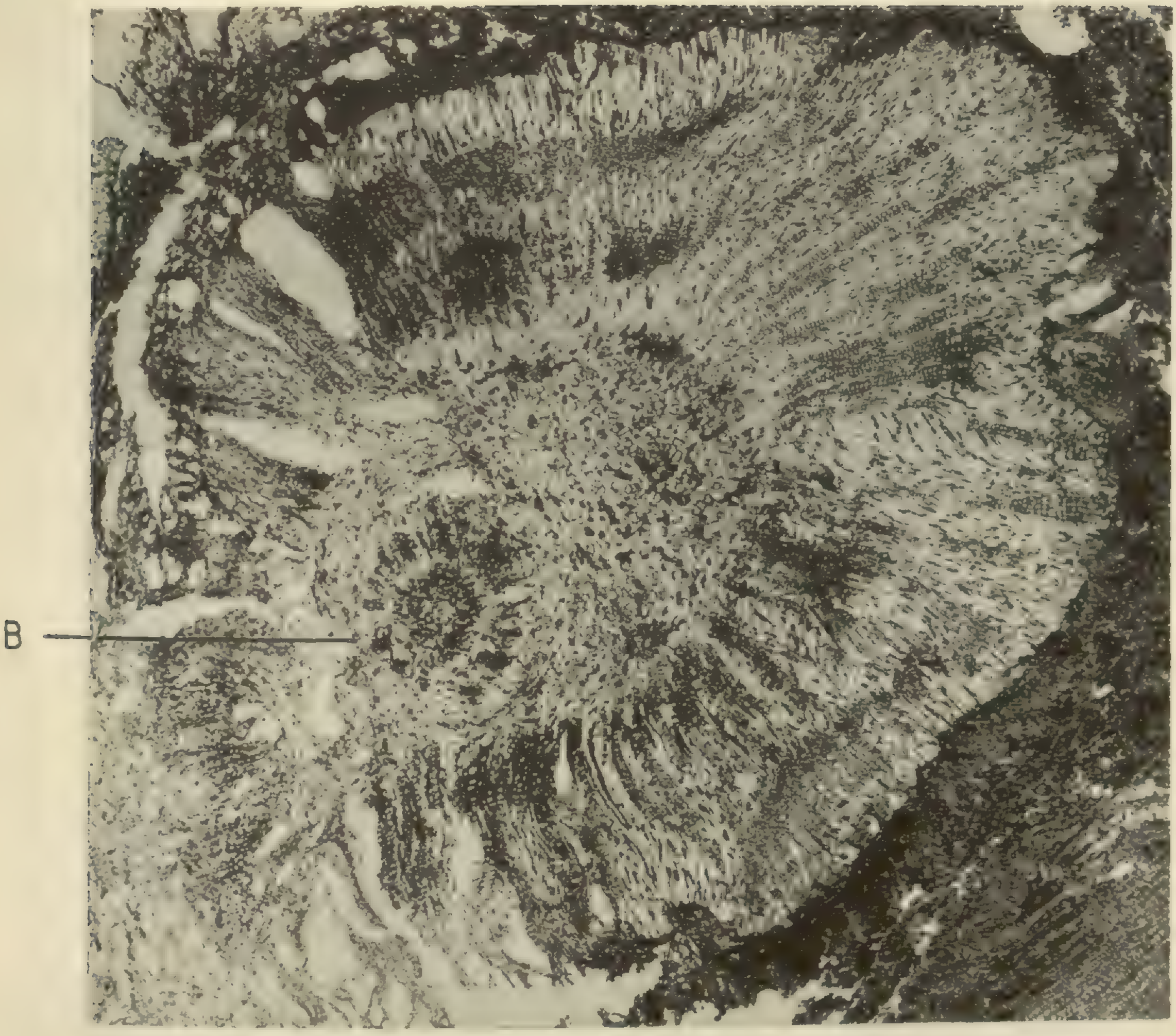
Explanation of Plate

PLATE 23

Medullosa grandis

Fig. 15. A single stele showing parenchymatous primary and secondary wood. Peel 718-C-t2. × 7.

Fig. 16. Portion of the secondary wood of a large stele showing high ratio of parenchyma. Peel 718-C-t2. × 8.5.



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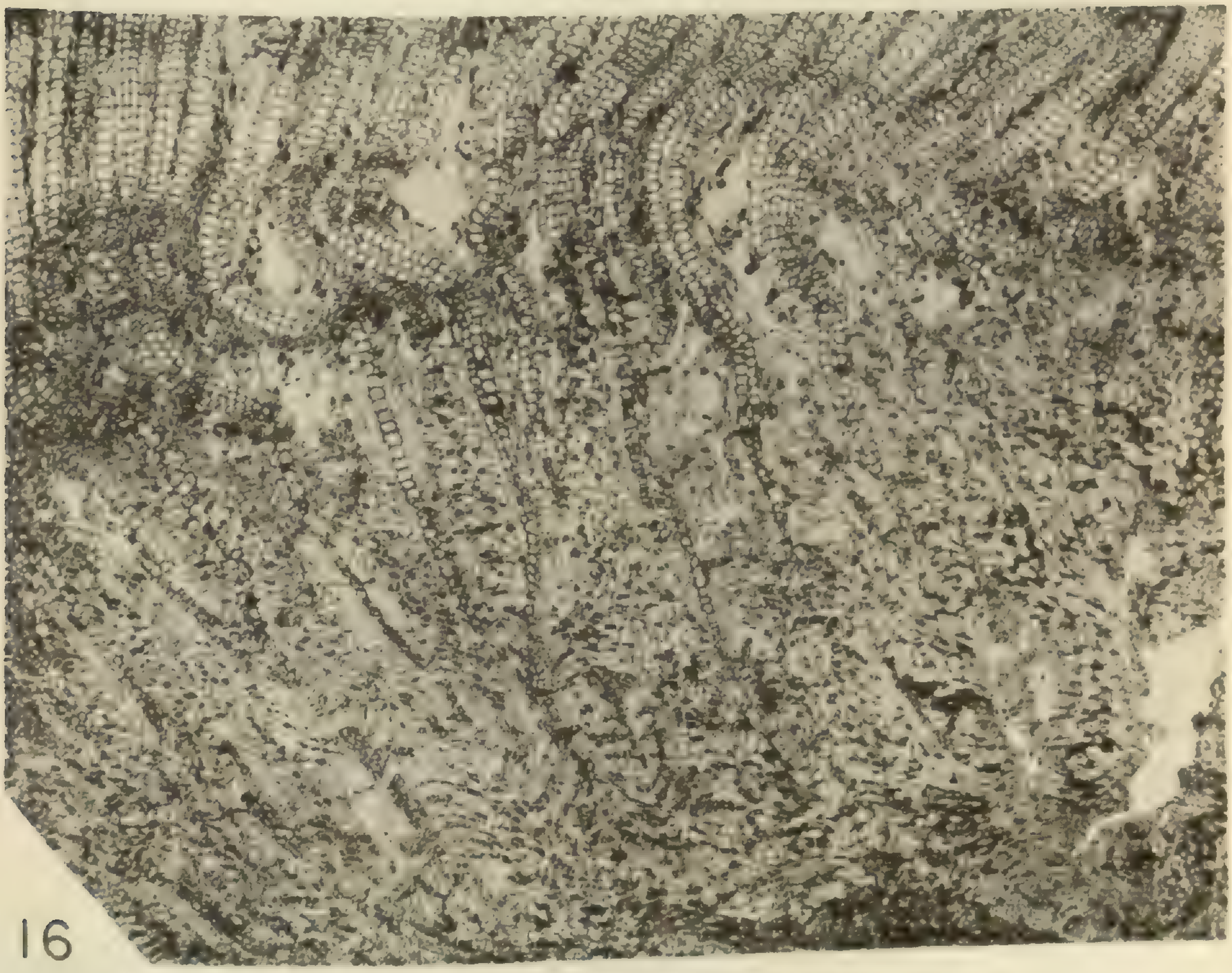

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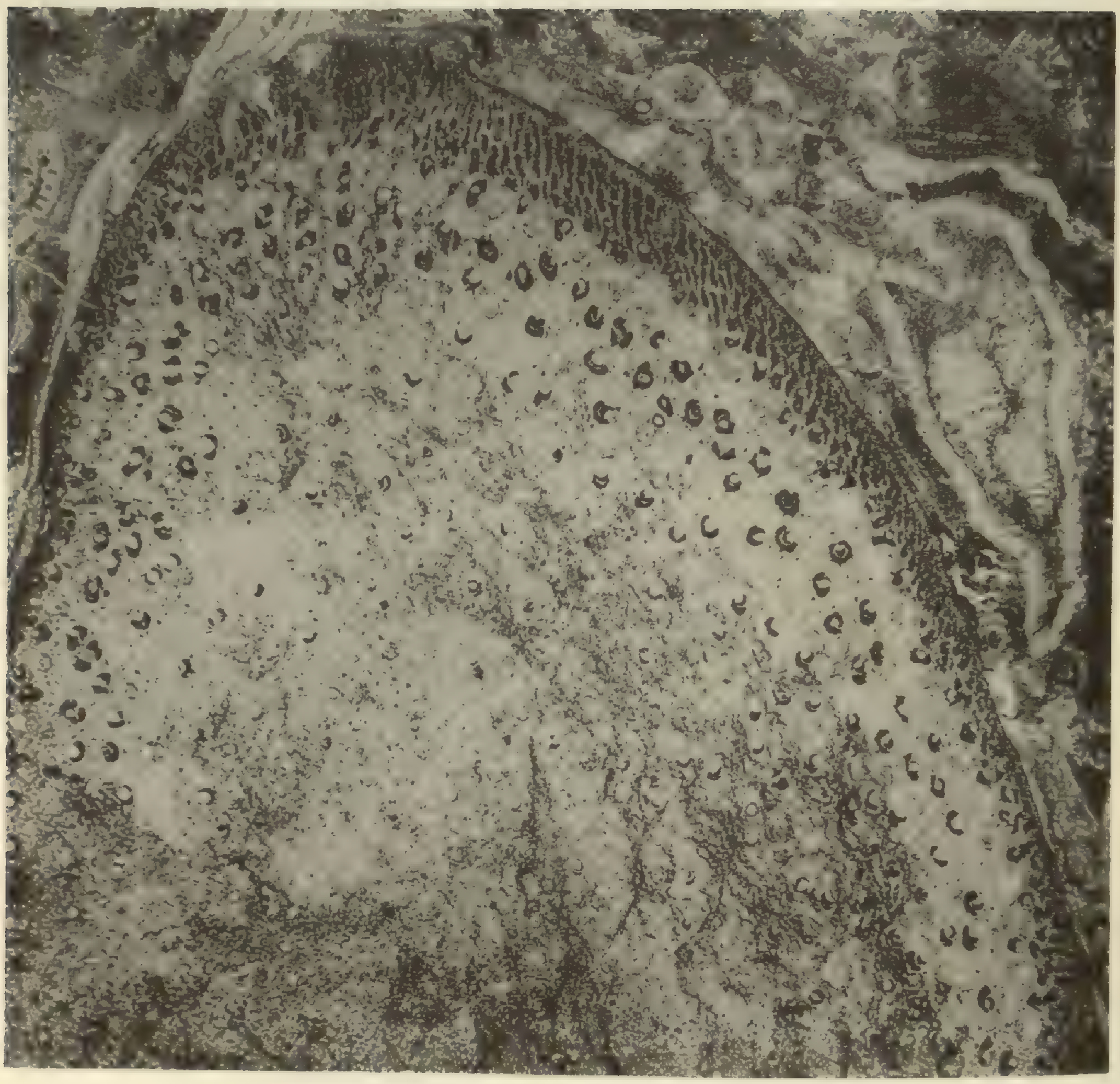
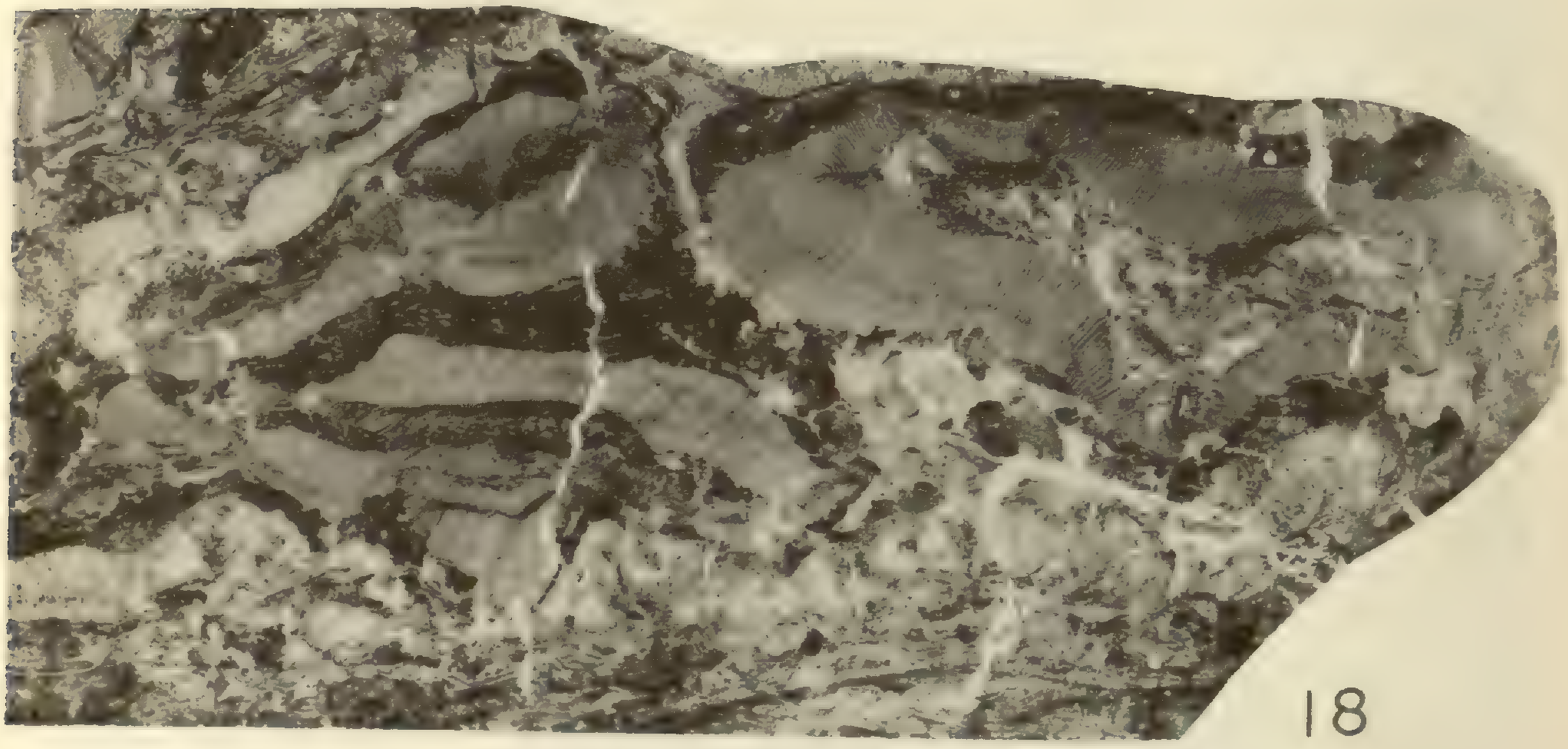
ANDREWS AND MAMAY — AMERICAN MEDULLOSAS





ANDREWS AND MAMAY — AMERICAN MEDULLOSAS

Explanation of Plate

PLATE 24

Fig. 17. *Medullosa distelica.* Transverse section of portion of a petiole. Peel 688-A-t4. × 5.5.

Fig. 18. *Medullosa noei* Steidtmann. Transverse section of stelar system. Peel 687-B-t1. × 0.9.

THE DISTRIBUTION OF *DIOSPYROS VIRGINIANA* L.*

HARRY R. SKALLERUP**

While the factors responsible for the present distribution of *D. virginiana* are in themselves not unique, the study of the literature pertaining to the native persimmon is particularly rewarding. Because the persimmon is both a fruit and forest tree the information obtained is increased two-fold. The combination of botanical, horticultural, and dendrological data answers some of the questions in regard to the determination and interpretation of the many aspects of its life phenomena. An attempt will be made here to present the factors affecting the macro- and micro-distribution of *D. virginiana* and to review and supplement certain aspects of the literature relating to them.

The genus *Diospyros* has a fossil record extending to the Mid-Cretaceous Era, and is represented by leaves, wood, calices, and even fossilized fruit, each having been reported from various locations throughout the world. Species evidently grew in Greenland, Siberia, Canada, northern Japan, Alaska, the British Isles, and in North Africa and Arabia (Berry, 1923). Although no major geographic region of the United States is without one or more fossil representatives of this genus, only one, based upon wood from a Pleistocene deposit in Louisiana, has been designated *D. virginiana* (La Motte, 1952). Yet it is reasonable to assume, in the light of leaf variation evident within the extant species, that perhaps a few others of the North American forms based on leaf remains and present as far back as the Cretaceous (Berry, 1923) may also be *D. virginiana*. Indeed, the present distribution pattern of *D. virginiana* indicates a very long history. In common with other plants of chiefly tropical affinity, it appears to have been dispersed throughout eastern United States from ancient centers in the Appalachian-Ozark highlands (Fernald, 1931).

Diospyros virginiana is now known only from the United States, and occurs within the area depicted in fig. 1. Each dot represents a county from which a collection has been reported. The apparent low density of collections in the Southeast can best be accounted for by a lack of records from this area. Thus, although only a few collections are represented from Mississippi, Alabama, and Louisiana, floras of these states list *D. virginiana* as occurring throughout the area. Moreover, a survey of the commercial stands of persimmon timber in the United States showed these states to be especially well represented (Fletcher, 1915). The critical collections at the periphery of its range are likely to define its extent fairly well, since specimens representing the rare species and new range extension are collected with a frequency disproportionate to their occurrence in the natural vegetation.

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*This paper is a portion of a monograph on the native persimmon, presented as a master's thesis in the Henry Shaw School of Botany of Washington University. Most of the bibliography of the original thesis has been retained since it includes some references not generally available.

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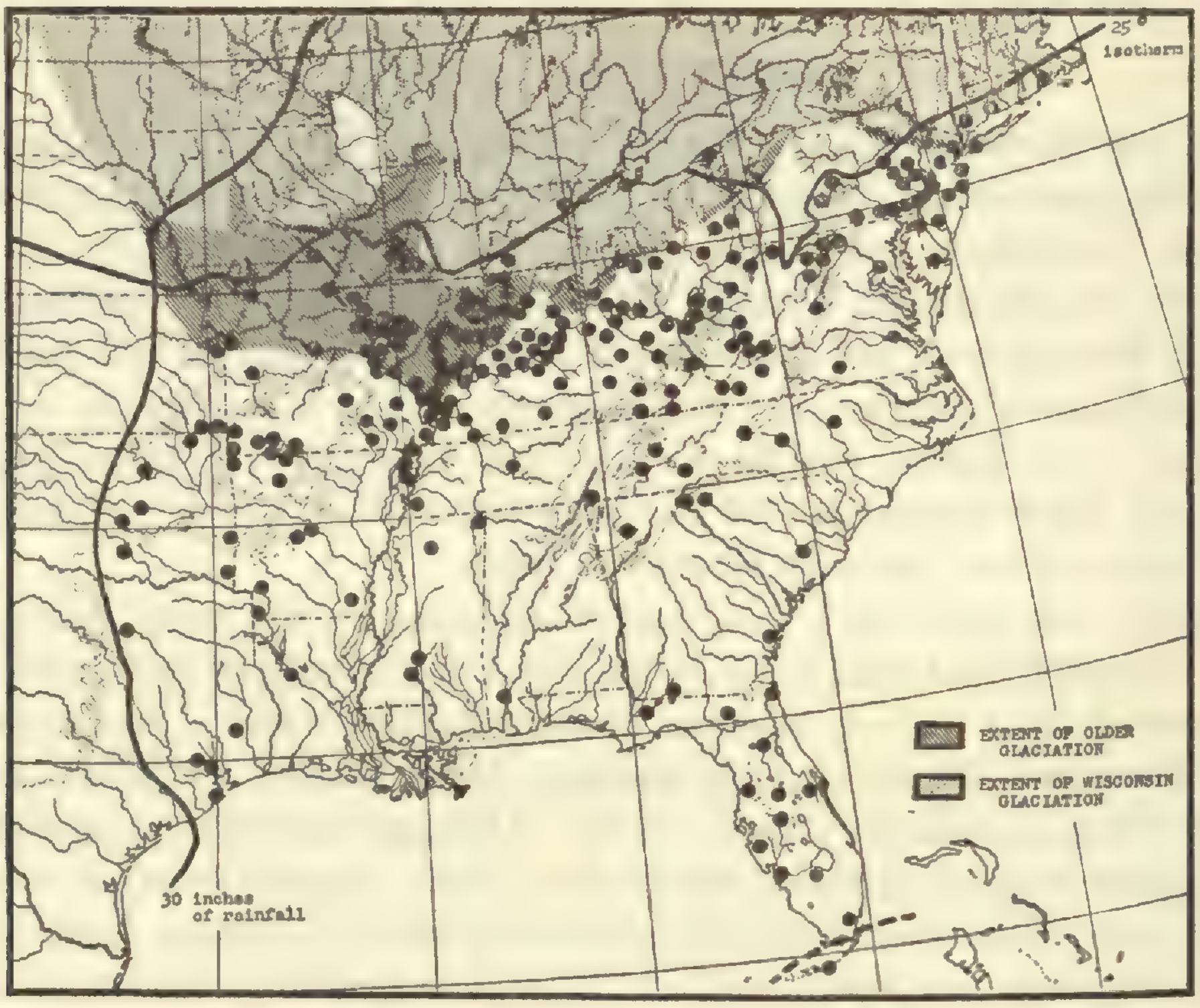

Fig. 1. Range of *Diospyros virginiana* L. Glacial and climatic boundaries drawn after Flint (1945) and Kincer (1922, 1928), respectively.

The study of the distribution of a tree such as *D. virginiana* has its disadvantages as well as its advantages. Specimens may be reported or collected from trees introduced outside the natural range, and although the trees may be hardy in these sites they could not have survived in nature as seedlings. Also, reports of non-fruiting specimens, particularly in the older horticultural accounts which ascribe non-fruiting to cold temperatures, may be erroneous due to the fact that *D. virginiana* is dioecious and some of the trees in question may be staminate.

Diospyros virginiana is found growing widely in areas of older glaciation (the Nebraskan, Kansan, and Illinoisan) and in the unglaciated area of the South. In the north and west of the older glaciated area *D. virginiana* appears to be limited by temperature and rainfall, respectively. Few specimens were found north of the 25° F. February isotherm as determined by Kincer (1928)[1]. Inasmuch as individual trees transplanted north of the 25° isotherm are able to survive and bear fruit, it seems that the photoperiod is not a factor in flower formation, and therefore does not limit its distribution (Naudin, 1880; Harrington, 1900; Trabut, 1926; Baldwin and Culp, 1941). It is possible that seedlings in the wild are unable to withstand the cold and to become established in such areas. This is supported by the report of Aikman and Boyd (1941) that persimmon trees planted for soil con-

[1]Of the series of maps prepared by Kincer (1928), February represents the coldest winter month for a period of 20 or more years.

servation purposes in southeastern Iowa (at the northwest limit of the range) needed a protected site if they were to survive.

In determining which factors might account for the western limits of the species, two possibilities appear: both the line of 30 inches of annual precipitation and an increase of 1000 feet in elevation running northward from the Edwards Plateau coincide fairly well with the distribution of *D. virginiana.* Since the persimmon is found commonly in the southern Appalachians (Eddy, 1927), it is more probable that the rainfall is limiting. (In the more northern mountains of Pennsylvania and West Virginia, persimmon is reported to be more rare than in the lowlands—letters from J. A. Small, E. L. Core—but here the lower winter temperatures and high elevations are probably responsible.) While it is not known at which phase of its growth the moisture requirement may be critical for *D. virginiana,* in other fruit trees it has been found that an annual precipitation of at least 30 inches is required by mature individuals (Magness and Traub, 1941).

While temperature and rainfall thus appear to limit the greater part of the range of *D. virginiana,* there is a conspicuous absence of specimens from the area of the last or Wisconsin glaciation within the compass of the 25° isotherm. That this area does not differ significantly in climate fails to explain the absence of *D. virginiana* in the later glaciated region. Berry (1923) states that during Pleistocene times the native persimmon retreated far to the south of the ice front, only to spread north again in the "wake of the ice sheet." With regard for the dangers in assuming that post-glacial expansion is still going on (Deevey, 1949), it would appear that *D. virginiana* had advanced into the glaciated area, only alternately to withdraw and advance in response to the Wisconsin glaciation, so that now it occupies the northern boundary of the older glaciation (where it is not limited by low temperatures) and has made but slight advances into Indiana, New Jersey, and Connecticut, the areas of the more recent glaciation. The isolated specimens in Indiana, Ohio, and New York (fig. 1) probably represent collections from cultivated trees, as does a specimen from Massachusetts (not shown on map—letter, R. Rollins, 1953).

Baldwin and Culp in 1941 made a cytological study of persimmon from selected stations throughout the range and found that two chromosome races are present: $2n = 60$ and $2n = 90$. Considering other members of the genus (Table I) it appears that the basic number of chromosomes is 15; accordingly the races of *D. virginiana* are regarded by Baldwin and Culp as tetraploid and hexaploid. Their relative distribution is interesting: the 60-chromosome race has a continuous distribution in the central and southeastern parts of the range, while the 90-chromosome race occupies a peripheral position throughout the rest of the range.

Several additional counts were made in this study. Collections of seeds gathered in St. Louis, Franklin, and Bollinger counties in Missouri, and from Washington County, Arkansas, were grown in the experimental greenhouse at the Missouri Botanical Garden. Chromosome counts made from aceto-lacmoid root tip squashes

TABLE I

SUMMARY OF KNOWN CHROMOSOME NUMBERS IN *DIOSPYROS**

Species	2 n	Source
D. discolor	30	Namikawa, Sisa, and Asai (1932)
D. texana	30	Baldwin and Culp (1941)
D. lotus	30	Namikawa and Higashi (1928)
D. kaki	90	Namikawa and Higashi (1928)
D. virginiana	60, 90	Baldwin and Culp (1941)

*After Baldwin and Culp, 1941.

showed these to have 90 chromosomes—the number reported by Baldwin and Culp in Crawford County, Kans., and Jasper County, Mo. While it would be premature to draw conclusions as to the meaning of the chromosome races in this species, it is of interest to note that the 60-chromosome individuals are found in and about the ancient eastern center of the species. The occurrence of higher polyploids on the periphery of the range is subject to two interpretations: (1) that they are autopolyploid derivatives which have been able to colonize areas not so accessible to the lower polyploid (Cain, 1944; Stebbins, 1950); (2) that the 90-chromosome race is actually of hybrid origin (with an extinct species or race) and is spreading eastward along the northern boundary of tetraploid *D. virginiana*. In either case, studies of both the morphology and cytology of plants of known chromosome number will be required before the question can be answered even tentatively.

In the course of horticultural practice *D. virginiana* has been introduced into climates outside of its natural range with varying degrees of success. It had been introduced into England before 1629. Parkinson's 'Paradisi in Sole Paradisus Terrestris' gives the first account of cultivated persimmon trees *(Lotus virginiana)*. One specimen given to George III by the Duke of Argyle (ca. 1790) and grown in the old Kew Arboretum was of considerable dimensions in 1895. At that time it was "apparently as contented [there] as in its native habitat" (For. and Gard., 1895). *Diospyros virginiana* has also been grown successfully in British Guiana (Hiern, 1873); it fruits regularly in the warmer European climates, although it is irregular in more severe climes where it has been reported to withstand temperatures as low as —25° C. (Naudin, 1880; Trabut, 1926).

FACTORS AFFECTING LOCAL DISTRIBUTION

Although the persimmon is frequently cited in the literature as a pioneer species —a tree that is among the first to grow in almost any situation—a survey of the flora growing spontaneously within the present city limits of St. Louis failed to show any persimmon trees growing in those abandoned places where a "pioneer" would be expected. That persimmons did grow in the area now incorporated as St. Louis proper is borne out by a few, but reliable, references. One of the most

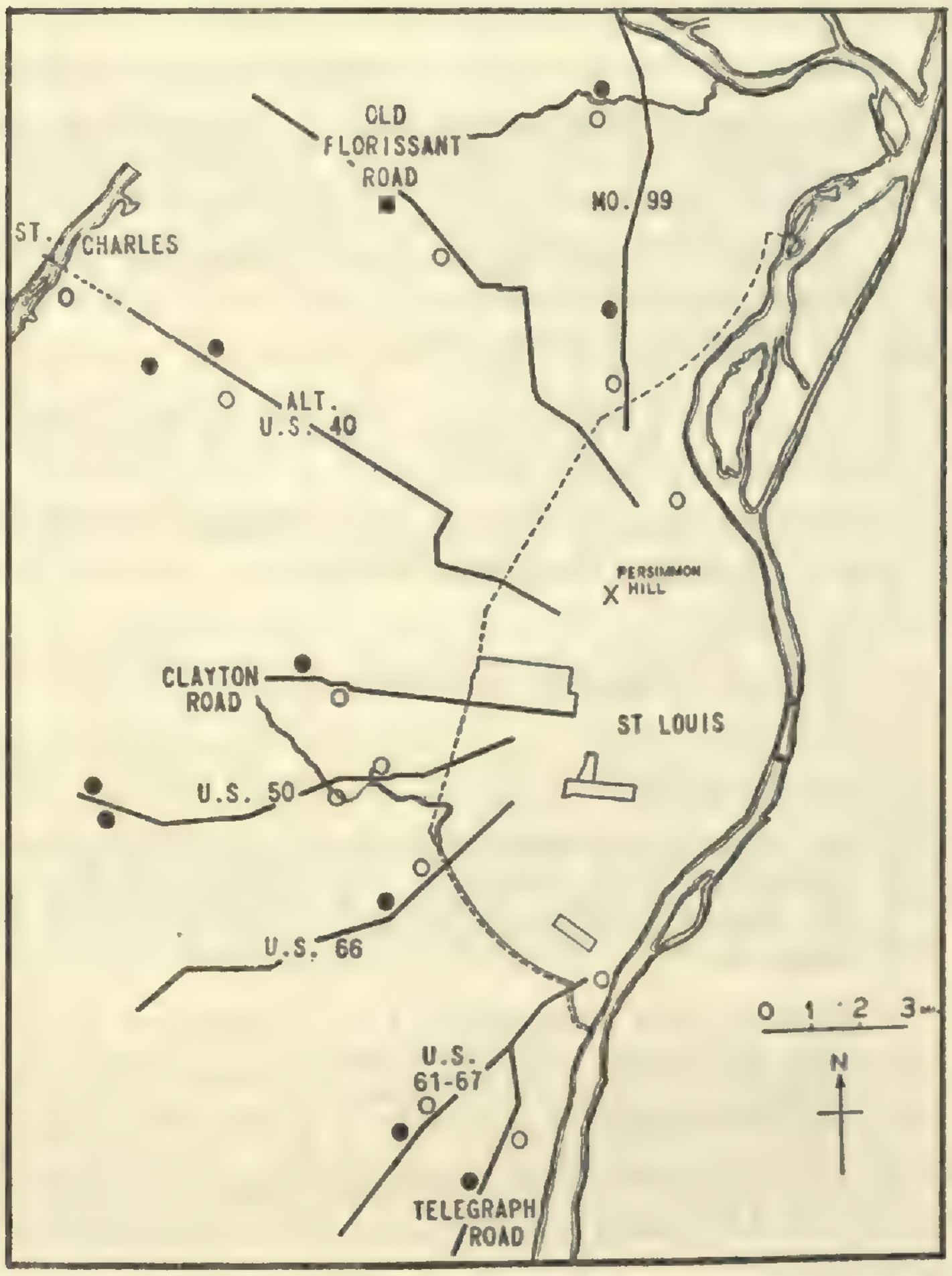

Fig. 2. Map showing occurrence of *D. virginiana* in the St. Louis area. Black dots represent sites where it was found closest to the city; circles represent apparently favorable sites where it did not occur.

interesting is the narrative by Elizabeth Kennerly Russell, 'Persimmon Hill'. Although written in the style of a saga, its title refers to the actual Kennerly mansion, *Côte Plaquemine*, built in 1832 on a hilly tract of land "five miles northwest of town . . . where Taylor and Kennerly Avenues cross today," and named for the persimmon trees commanding the site (Russell, 1948). Prior to this time the land outlying St. Louis that was not upland forest had been kept in prairie by the Indians who annually burned the vegetation in order to flush out game. By 1836, the prairies had practically disappeared, due to the cessation of the autumnal fires and were succeeded by young forests (Beilmann and Brenner, 1951).

Nicholas Riehl, collecting in 1838, gathered persimmon specimens from the "fôrets" of St. Louis; while a visiting farmer, Patrick Shirreff, tasted his first persimmon upon travelling Old St. Charles Road, only to mention its disagreeable taste in a letter written home, dated 1835 (Stevens, 1906). Coincidental in time and place with references to the flora are necessarily those to the birds and animals of the region about which William Kennerly reminisces ". . . we learned the ways

TABLE II

Road	Sites where *D. virginiana* was found (represented by black dots, fig. 2)	Sites where *D. virginiana* was not found (represented by circles, fig. 2)
I. U.S. 61	(1) Clone, on top of slope at edge of old field with 5, 7* (2) Individuals in grove with 2, 4, 8	Mixed oak association
II. Telegraph Road	Scattered, on top of ravine, s.w. side in mixed oak woods	Flood plain of Mississippi River
III. U.S. 66	(1) Clone, same as I (1). (2) Scattered, in grove with *Pinus echinala*, 1, 2, and 6	Mixed oak association
IV. U.S. 50	Clone, on slope of old field at edge of grove of *Ulmus*	Along River des Peres
V. Clayton Road	Scattered, in stand of 1, 2, 3, 4, 8, and *Cornus* sp.	Brier thicket in recently cleared field
VI. Alternate U.S. 40	(1) Clone, slope of old field, with 5, 7, *Andropogon virginicus, Aster* sp. (2) Individual in mixed oak association	(1) Flood plain of Missouri River at St. Charles (2) Mixed oak association
VII. Old Florissant	Scattered, along ditch with 4, 5, 7, *Rhus glabra, Populus deltoides*. Also, specimen of *D. virginiana* var. *pubescens* found here	Mixed oak association
VIII. Missouri 99	Scattered, side of road, with 2, 4, 6, 8, *Rhus glabra, Prunus* sp.	Dense grove of *Ulmus* at edge of cultivated field
IX. Missouri 109 (not on map)	Scattered, on glade with *Bumelia lanuginosa, Cercis canadensis*	

*1. *Acer Negundo*
2. *Celtis occidentalis*
3. *Platanus occidentalis*
4. *Quercus* sp.
5. *Rubus* sp.
6. *Sassafras albidum*
7. *Symphoricarpos orbiculatus*
8. *Ulmus americana*

of animal life in the woods and meadows . . . we could read the small dainty hoofprints of the deer as well as the bobcat's heavier tread . . ." (Russell, 1948). Wild turkey, deer and abounding game were also written of by Flagg in 1836 (Thwaites, 1896–1901; see also Beilmann and Brenner, 1951, for a more complete account). However, with the expansion of the city, persimmon became scarce within its limits. In 1911 the Engelmann Botanical Club listed *D. virginiana* occurring in St. Louis proper only in such floral sanctuaries as Missouri Botanical Garden and in Tower Grove and Forest parks (Engelmann Bot. Club, 1911).[2]

[2] Unfortunately the origin of these trees, like plants in many parks and botanical gardens, is speculative. Among the trees in the nursery of Tower Grove Park in 1871, fifty were listed as being persimmons (Shaw, 1871). Henry Shaw, in addition to purchasing the Riehl collection of herbarium specimens, also bought the first trees planted in his Garden from the Riehl Nursery (Spaulding, 1909).

Ironically, a year later persimmon was recommended as a native tree suitable for growing in St. Louis (Jensen, 1912).

To determine the present occurrence of persimmon in the St. Louis area, a reconnaissance was made along the main highways radiating from the city. Although every side road could not be followed, and doubtless, in the forced pace of highway traffic, some trees were overlooked, a fairly complete idea of its local behavior was obtained. Figure 2 and Table II summarize the data obtained. It can be seen that persimmon does not occur within the city limits, and is primarily an upland tree which prefers an open drained habitat. *Diospyros virginiana* was usually found growing in clones or scattered in open situations where there is little competition; or else it was found scattered with other second growth trees or in young mixed-oak forests (pls. 25 and 26). In the former instance, the trees were young and were initiating growth, while in the latter instances they were comparatively old or dying and represented the last of their number. The present local absence of persimmon within the metropolitan area can not be explained on the basis of unfavorable habitat brought about by smoke or industrial gases, for trees are successfully grown as ornamentals in the city parks and at the Missouri Botanical Garden. Rather, the lack of dispersal agents for its seeds appears to be the underlying cause.

Persimmon is poorly equipped for dispersal by means other than animals, or, indirectly, by man. The fruit, a true berry, ranges from ¾ to 1½ inches in diameter, and bears proportionately large seeds, four to eight in number. Once separated from the pulp, the seeds are not light enough to be scattered by wind or to float upon water. In the city they can still be seen under cultivated trees, untouched by squirrels, rabbits, or rats, as late as June. Tables III and IV list the animals that eat persimmon fruits in the wild. Although these data do not show diet preferences, the fact that the animals listed do eat persimmon fruit indicates that they act in a large degree as dispersal agents for its seeds, since it is unlikely that the seeds are dispersed by any other means. In addition to the animals listed, the pine mouse will use the seeds as food (Martin, 1951), while the meadow mouse is known to include persimmon and *Bumelia* seeds among its caches, and thus figure in its dispersal (L. G. Brenner, personal communication, 1953). While certain birds eat the flesh or pulp of the fruit, it is doubtful whether any listed in Table III B (except the turkey now rare in Missouri) is able to swallow or void the large seeds. This is in contrast to sassafras (*Sassafras albidum* (Nutt.) Nees), a "pioneer" species which does grow spontaneously within the city, whose fruit and seeds are eaten by birds and thus is scattered more widely than persimmon.

TABLE III

LIST OF ANIMALS AND BIRDS EATING PERSIMMON FRUIT*

Species	Per cent of Diet	
	Southeast	Northeast
A. Animals		
Red Fox	10–25	0.5–2
Gray Fox	2–5	0.5–2
White-tailed Deer	0.5–25	Not recorded
Opossum	2–5	Not recorded
Raccoon	5–10	5–10
Ring-tailed Cat (Texas only)	5–10	———
Striped Skunk	0.5–2	Not recorded
B. Birds		
Wild Turkey	Not recorded	0.5–2
Catbird	Not recorded	2–5
Robin	2–5	Not recorded
Yellow-bellied Sap-sucker	Not recorded	Food item of undetermined extent
Myrtle Warbler	0.5–2	0.5–2
Cedar Waxwing	2–5	Not recorded
Mockingbird	Not recorded	Food item of undetermined extent

* Based upon stomach and crop analyses, droppings, and field observations (after Martin, 1951).

TABLE IV

OCCURRENCE OF PERSIMMON IN MISSOURI WILDLIFE*

Species	Samples examined	Occurrence of persimmon
Deer	348 stomachs	40
Coyote	680 stomachs	51
Red Fox	731 stomachs	31
Gray Fox	251 stomachs	56
Quail	5,472 crops	33
Quail	1,358 droppings (roost)	1

* Prepared from letter, L. J. Korschgen, Missouri Conservation Commission, 1953.

HABITAT TYPES

As mentioned above, *D. virginiana* was found either initiating growth in abandoned places or as a minor element in mixed-oak associations. To interpret its behavior in these habitat types, data will be presented from sites where more complete studies were made.

Old Fields.—Many authors list *D. virginiana* as occurring in clones along roadsides, in old fields, and other waste places (Sargent, 1894; Eddy, 1927; Van Dersal, 1938; Steyermark, 1940). Personal observations were made along roadsides and in old fields at the Missouri Botanical Garden Arboretum, Gray Summit, where

information concerning the history of the land is fairly complete. Here, three patterns of "field invasion" were found to be present. These may be characterized as:

(1) Clonal: trees of varying ages, all of the same sex.
(2) Clonal: trees of almost the same age, all of the same sex.
(3) Scattered: trees of varying ages, both sexes present.

(1). A group of the first type was found in a sloping field, abandoned since 1924, which, except for the eradication of elm, had been allowed to grow wild (A. P. Beilmann, personal communication, 1953). An apparently injured, double trunked tree, near a shallow gully, was the oldest element present (c. 20 years). Growing in association with it were *Andropogon virginicus, Allium* sp., *Panicum,* sp., *Aster* sp., *Solidago* sp., young *Juniperus virginiana, Cornus racemosa,* and *Parthenocissus* sp. In somewhat elongated concentric arcs about the old tree were other persimmon trees of different ages, the younger ones being on the periphery, but more numerous down the slope (pl. 25). Trees old enough to bear fruit showed the single peduncles characteristic of pistillate trees. Upon digging near the bases of several older trees, long horizontal spreading roots[3] connecting the older trees were found at a depth of a foot (pl. 25). Several roots were followed for their entire lengths and were found to branch repeatedly. These gave rise to several small trees, one of which is shown in pl. 25. The diameter of the root remained almost constant (¾ inch) except near the tips, where normal growth occurred. There were no evidences of decay or separation of root branches; nor were the branches themselves chance root grafts. From observations of other sites similar to this one (Table II) it was noted that the advance of the younger trees is usually more rapid down the slope, probably due to the greater development of the root system in this direction, a consequence of gravitational influence or greater soil moisture. Although the aspect of this site was largely clonal, a few of the smaller trees may have been seedlings, since seeds collected here were found to be viable.

(2). The second group was observed along a roadside near an abandoned field of similar history to the one above, except for possible disturbances due to road repairs. Other species growing at this site included: *Rhus glabra, Symphoricarpus orbiculatus, Rubus* sp., *Andropogon virginicus,* and *Rudbeckia* sp., as well as a few very young *Juniperus virginiana* trees. The largest persimmon trees examined here were all essentially the same age (about 15 years). They exhibited the uniform growth characteristics and the same sex of trees vegetatively propagated from a common stock, yet no "parent" tree as in the above situation was present (pl. 26). These trees were also found to be connected by stolons, while some individuals had their own groups of younger trees about them. Seeds found at this location were also viable. It is conceivable that this situation was brought about as a result of the

[3]There are references to persimmons as "stoloniferous" (Sargent, 1894; c.f. also, Holm, 1909). However, a complete description of this condition was not found in the literature. The roots described here did not appear to differ in gross structure from the normal roots.

roots of an older persimmon tree having been accidentally cut into pieces and distributed, so that groups similar to those of the first type were concentrated in this small area. That this is possible is demonstrated by a common horticultural practice in which cuttings of persimmon are made for propagative purposes and vigorous sprouts are obtained from them. Further, decapitated trees have been reported to send up root suckers within two months after being injured (Fletcher, 1915).

(3). On the top of the slope of the same field, but away from the road, a third pattern was found. Here trees of varying ages and forms were scattered in groups. Most of the trees were from 15 to 25 years old, although some seedlings were also found. The trees were both staminate and pistillate, and occurred in sporadic groups over the field. Most groups were composed of two or more trees, although some lone trees were noted. Ecologically, this site is part of the "highway" system used by deer and other animals at the Arboretum (Beilmann, personal communication, 1953). The scattered, but grouped trees closely reflect the way seeds are dropped by animals. Yet it is difficult to account for their non-clonal habit. The most likely explanation is that none of the trees were ever injured to the extent that they began to sucker. No plowing had been done in this field for over 25 years and the trees were not planted out. Injury by cattle grazing (besides trampling) is speculative; there are reports that cattle will not browse persimmon leaves or twigs (presumably because of calcium oxalate crystals and tannins present—Deam, 1932; Van Dersal, 1938); however, they are known to eat the leaves when suitable forage is not available (Brenner, personal communication, 1953), and many wild animals are reported to eat the buds and leaves (Missouri Conservation Bulletin, 1940).

Forest associations.—From observations at the Missouri Botanical Garden Arboretum and in the St. Louis area, persimmon was never found upon a river flood plain (Table II), nor were mature trees ever found in a pure stand. Persimmon is frequently mentioned in the literature as existing in pure stands and as reaching its greatest proportions in the basin of the Mississippi River and along the Wabash River Valley. Ridgway (1882, 1894) and Sargent (1894) are probably the uncited sources for these references. However, a more recent survey of the hardwoods growing in Louisiana listed persimmon as only a minor species in all the habitats in which it was found (Lentz, 1929; Hepting, 1936), while Miller and Tehon (1929) report that no persimmon trees as described by Ridgway are now known in the Wabash Valley. Evidently, persimmon was more of a dominant tree (as were others) in the primeval forest than it is in the second growth timber of today.

That *D. virginiana* is only a minor element in present-day associations is verified by other authors. In the Ozark and adjacent plains region, Steyermark (1940) found *D. virginiana* occurring as a pioneer element on dolomitic glades, as a temporary dominant on bald knobs and bare limestone areas, and, frequently,

initiating oak-hickory associations on the acid substrata of the prairie. However, he did not list it as a member in the building of a flood plain climax, in associations where burning-over had recently taken place, or in drainage regions. Palmer (1921) did not mention *D. virginiana* as a conspicuous element of the flora of the Ozarks. Although Lentz lists the persimmon as growing in both the well- and poorly-drained bottomlands of northeastern and southern Louisiana, it was not mentioned as occurring in the Louisiana swamps or in lands subject to overflow. In the Carolinas, Eddy (1927) found it growing at the edge of alder swamps and on the coastal plain, but again, only as a minor or subdominant species.

This evidence indicates the wide range of ecological situations in which *D. virginiana* is able to initiate growth; yet, because of its slow rate of growth, it is shaded out by faster-growing trees. Brenner (1942, 1952) made comprehensive observations of the mixed oak associations in his environmental and quadrat studies at the Gray Summit Arboretum. An example of the short duration of the persimmon in an open woodland can be found from data reported by Brenner from a quadrat staked out in an oak coppice in 1937. At that time, numerous persimmon and other heliophilous trees were keeping pace in growth with the white oaks, the dominant tree. Since then, the white oaks made considerable growth, with the result that, 15 years later, one-fourth of the persimmons were dead and the remaining ones were in poor condition.

SUMMARY

1. Although formerly members of the genus *Diospyros* ranged far to the north, the native persimmon now appears to be limited in its spread to the north by an annual temperature of 25° F., and to the west by rainfall of 30 inches annually. Within these limits, however, it appears uncommon in the area of the Wisconsin glaciation.

2. Supplementary chromosome counts from Missouri (three counties) and Arkansas (one county) are in agreement with previously recorded determinations.

3. Local absence of *D. virginiana* is attributed to eradication of the trees that were present in what is now the city. Dispersal of seeds is largely through the activities of animals, and for this reason persimmon is not known as a pioneer species within urban limits.

4. Three types of "field invasion" by persimmon in abandoned places are described. The ability of the roots to sucker upon injury accounts for the dense clones often found in these situations, although non-clonal situations also exist.

5. Although persimmon once was known to occur in pure, dense stands, more recent reports indicate that this is now not the case. Throughout its range persimmon is reported as a minor species in older associations.

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Explanation of Plate

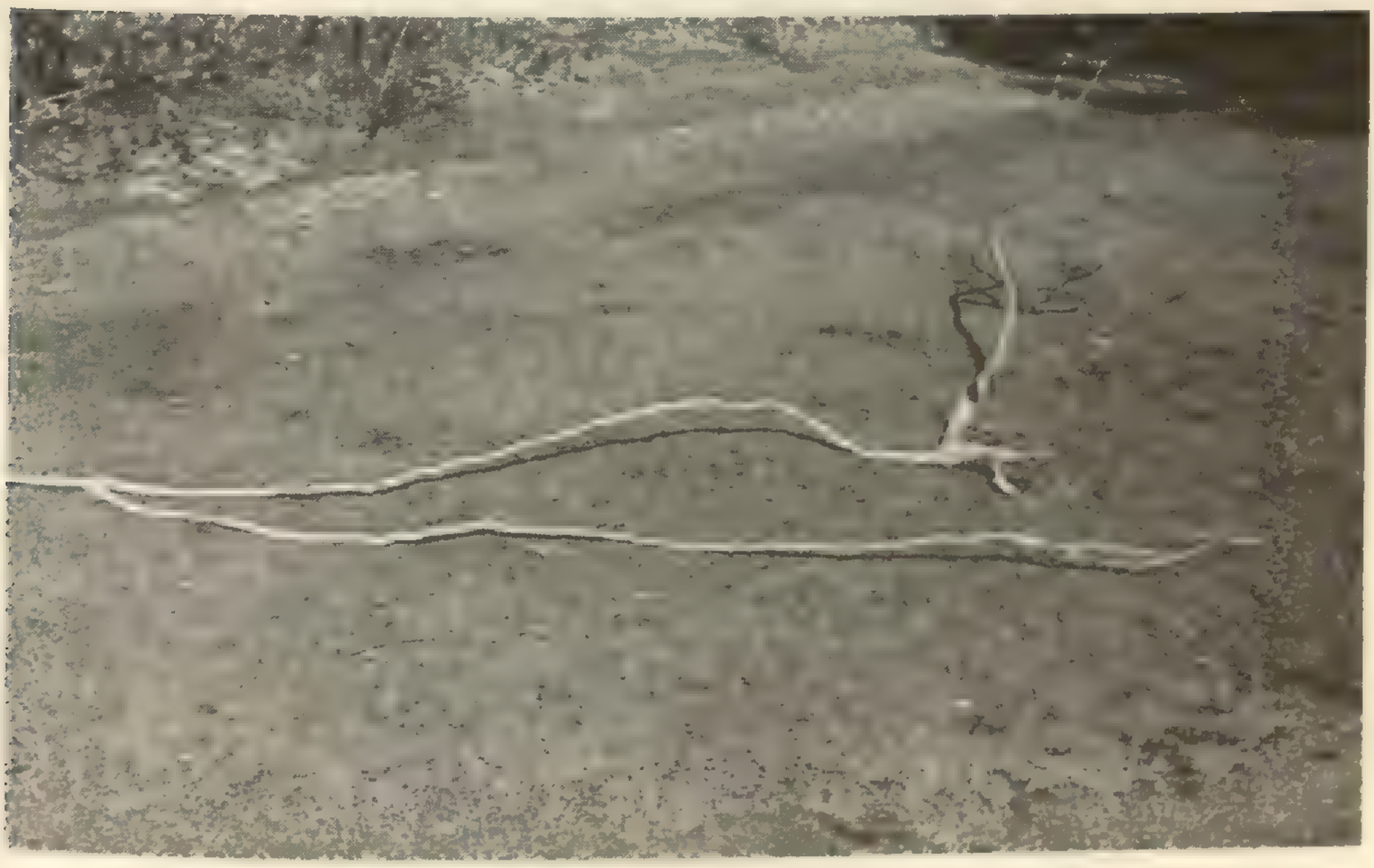
PLATE 25

Diospyros virginiana L.

Fig. 1. Clonal type 1: Trees are of varying ages, and same sex.

Fig. 2. Portion of a "stoloniferous" root from the above situation showing its branching nature and one young tree attached to it. (Length of root approximately 6 feet.)

1



2

SKALLERUP—*DIOSPYROS VIRGINIANA* L.

1

2

3

SKALLERUP—*DIOSPYROS VIRGINIANA* L.

Explanation of Plate

PLATE 26

Diospyros virginiana L.

Fig. 1. Clonal type 2: Trees are essentially the same age, and are of the same sex.

Fig. 2. Tree group characteristic of the third type.

Fig. 3. Persimmon in mixed oak association.

WILDWOOD
A STUDY IN HISTORICAL ECOLOGY

ALFRED G. ETTER*

Prologue

This is the story of a gathering of towering trees, old spreading oaks and sky-penetrating hickories that shelter the past in their shade. It is one of the few old woods that remain on the rich uplands that lie northwest of St. Louis between the Missouri and Mississippi rivers. Most of the scattered timber that early settlers found on the headwaters of the creeks in this area was cleared to make fields, or cut for cabins, firewood, fence-posts, lumber, cooperage, or one of the many other purposes for which wood was used during that period of American expansion which so depended on its omnipresence. A few wood-lots, through the smile of fortune, were preserved on tracts of land belonging to large estates. Wildwood was one of these estates, and it took its name from one of these old woods.

History

In the earliest days of the frontier when the land took men and hid them in the shadows of its trees, or lost them on its seas of grass, Wildwood's acres stood ignorant of everything but Indians. Then French forts began springing up along the near-by Mississippi. The French town of St. Louis was founded in 1764. Shortly thereafter Spain assumed control of this Upper Louisiana region. Then near the end of the century the Spanish regime began to yield to the pressure of the American movement west. Grants of land were made by the Spanish to many early frontiersmen and explorers, among them Daniel Boone. Settlements were also recipients. The village of Florissant, a few miles north of Wildwood, received a large gift of land for its common fields and wood-lots, about 1785.

It was around the time of Christmas in 1799 that the Spanish Lt. Governor, Don Carlos Dehault Delassus, granted to John Wendel Engel a tract of 800 arpens (680 acres) lying on the river Maline. Wildwood (to be) was in the northwest corner of this grant, and so first became a parcel in the domain of Man. By 1804 John Engel was apparently stirred by the ever-ready lust for money, for in January he sold 600 arpens of his land to James Rankin for 500 dollars. The other 200 arpens, including Wildwood, he reserved for himself for cultivation. The Spanish regime ended officially in March 1804, and the great territory of Louisiana became American. Whether or not this influenced Engel in some manner is not certain, but in August of that year he completely gave up his ideas of farming by the river Maline and sold to Simon Wood the remaining land, including that destined to become Wildwood. During his brief period of residence Engel had built a house and cleared ten arpens of land and put it under fence. The 200

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arpens, house, and improvements, together with a spring, went for the price of 200 dollars.

After the transfer of the capital of the Territory of Louisiana to the City of St. Louis, the old fur post became an active and growing city and the headquarters for expeditions and vagrant dignitaries of every description. Simon Wood held his property for sixteen years, but during this time entered into some contract with a gentleman named Josiah McClenahan. Wood could not fulfill the terms, and was obliged in the spring of 1820 to sell his farm to McClenahan for 500 dollars. John Mullanphy had entered into a covenant previously for the purchase of the same land from McClenahan for 750 dollars, as soon as the latter should obtain a clear title to it. This shrewd deal was accomplished just before Missouri received its statehood in 1821.

In 1830 Mullanphy provided that the 200 arpens on Maline Creek should be the property of his young grandson Owen Chambers. It was agreed that should Owen die before the age of twenty-one the land was to revert to Owen's brothers and sisters (of whom there were to be twelve)! Owen did die before he was 21, and in 1850 it was necessary to divide the Maline property. Fortunately Mullanphy had meanwhile procured the 600 arpens of land which were a part of the original grant, so that when the division became necessary there were 800 arpens to be divided among the eight children interested.

To make a complicated story simple, of the resulting eight lots, lots Nos. 7 and 8 contained the 200 arpens of Simon Wood's farm. Lot 7 went to Ellen Chambers LaMotte, wife of J. H. LaMotte, ultimate owner of Wildwood. Lot 8 went to John Chambers, who in 1851 sold the property to LaMotte, and so the original plot of 200 arpens was once more consolidated. The price paid for 110 acres was $3,292.

At the time of the purchase LaMotte was a major in the United States Army and only five years before had been actively engaged in the battles of the Mexican war. He continued his service until 1856, striving assiduously (as he expressed it in letters written at the time and preserved in the library of the Missouri Historical Society) to make the necessary preparations for a happy life on his Maline land. These preparations included the careful sale of many of his investments in property in St. Louis and elsewhere. During this time his farm was run by various tenants, as it had been in the years before it came under his ownership. When he resigned from the army he proceeded immediately with his plans for the transformation of these 220 acres into a home and estate. Work was begun on the construction of his seventeen-room home. Stables, quarters for slaves, and miscellaneous buildings slowly began to rise from mere vision to the reality of Wildwood, country estate of J. H. LaMotte.

Then came the interruption of the Civil War and its attendant complications. Actually it was not until 1867 that the LaMotte family was established in the new home. At that time LaMotte, visiting in Georgetown, received a letter from his son, Frank, to the effect that "We are well and comfortably fixed at Wildwood,

plenty to eat, drink and smoke. Carpets down, potatoes all in, fences up. Harry and mother ride out frequently and enjoy the country very much . . . Uncle is furnishing our apartments in princely style—marble mantels, paper etc."

It was in keeping with the wishes of Major LaMotte that the woods around the house were never cut, though horses, cows and sheep grazed at various times through the undergrowth. Meadows of timothy and fields of corn occupied the flat valleys north of the river Maline. On fertile slopes tobacco was planted and nearer the house were peach orchards, rows of potatoes, and sun-filled patches of watermelons for which the Major became famous. The raising of horses became his particular pastime, and their grazing, combined with that of the sheep and cows, soon made a spacious park from the woodland about the home.

The Victorian refinement of the secluded Wildwood home held sway in luxurious comfort, peace and plenty while Major LaMotte lived. After his death in 1892, his wife and few remaining members of his family continued to live in the home, but his many activities were no longer attended. A tenant farmer ran a few cows in the extensive pastures, but apparently not enough to keep many young trees from sprouting. In 1911 Mrs. LaMotte died and the property went to her daughter, who passed away within a month. Her husband lived alone in the mansion for a few years, leading an almost hermit-like existence, neglecting the home and the fields. At his death, the home stood alone in the woods, forgotten except by vagrants who found the old place a haven on winter nights. There was no caretaker and no interested heir.

In the meantime a new tenant farmer had moved on the property and began building up his dairy herd. According to his recollection, about 1920 he found it necessary to enlarge the available pasturage. Portions of the woods that had grown scrubby were cleared, and the really dense areas in the valley that had never been pastured at all were also cleaned out. Fallen trees and logs were burned, and the cows turned in to finish the work. Mr. S. still resides on the acreage and pastures his cows in Wildwood.

Until 1929 the LaMotte mansion at Wildwood remained abandoned. At that time it was sold to the present owner who removed seven rooms and restored the rest. His purchase included only that land in the immediate vicinity of the house. The remainder (about 200 acres) was sold at public auction in 1934 for $60,000. The purchaser intended to build a private home on the grounds, but his plans did not mature, and during 1946 a "For Sale" sign went up, offering 180 acres for $180,000! The price of this land had thus risen from approximately $1 an acre in 1804, to $3.00 and then $4.50 in 1820, $30.00 in 1851, $300.00 in 1934, and $1000.00 in 1946. Once it was free!

The pressure of suburban development has finally risen to the point where Wildwood can scarcely hope to exist longer as a unit, much less as a farm, within city limits. In this respect, this study is essentially an obituary.

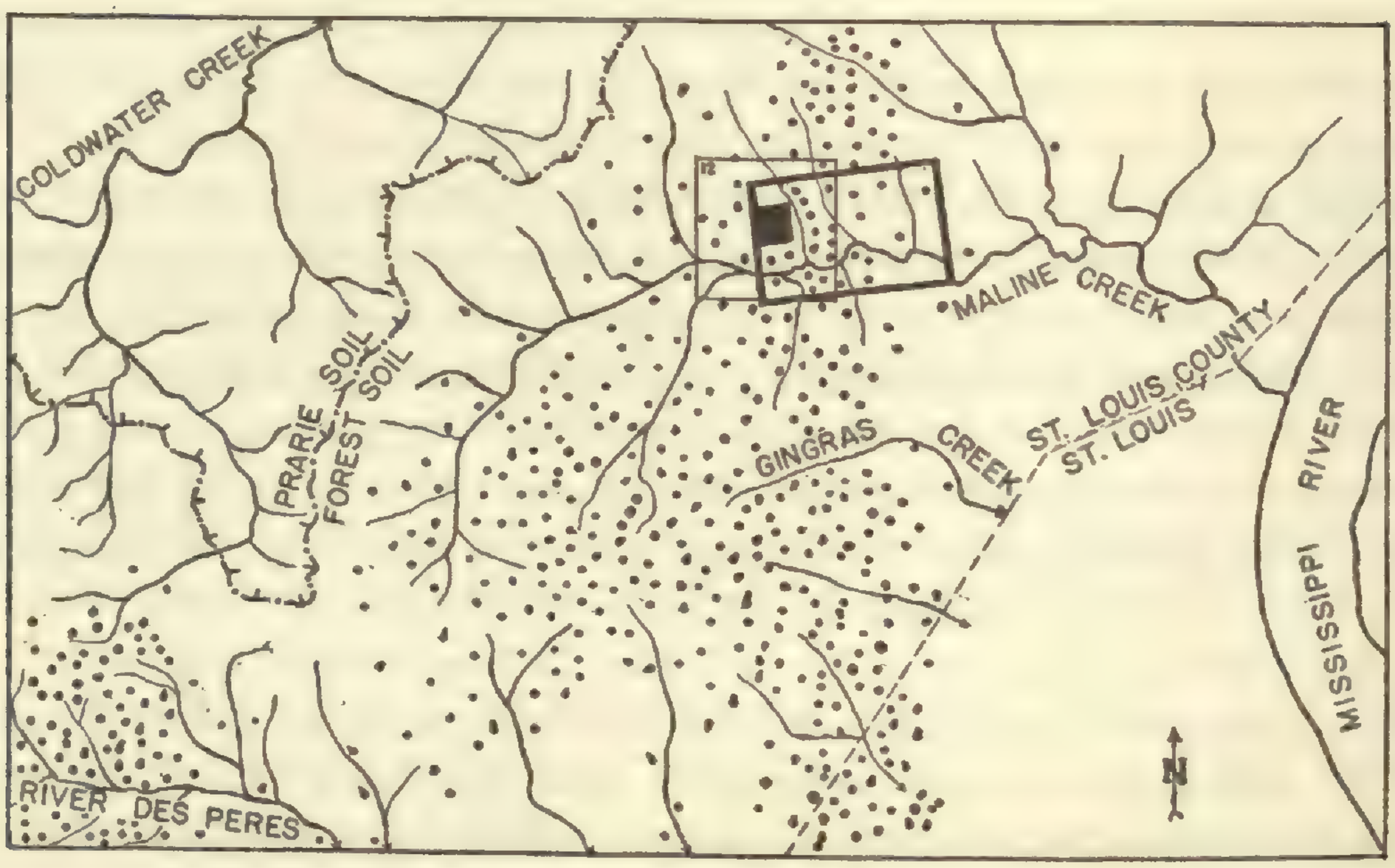

Fig. 1. Prairie and timber areas northwest of St. Louis as recorded by surveyors in 1817-1818. Timbered areas dotted; prairie areas unmarked; no survey data were at hand for the extreme northeast corner of map or for St. Louis proper. Original Spanish grant outlined in heavy black; Wildwood proper is solid black. Square area lightly outlined and marked 12 is Section 12 in Township 46 North, Range 6 East. The town of Ferguson centers on the west boundary of Section 12. St. Ferdinand de Florissant is about 3 miles northwest of Wildwood. The prairie soil boundary is from Krusekopf, 1923.

EARLY DESCRIPTION

Figure 1 shows the original Spanish grant in heavy outline, and Wildwood (the wood-lot and residence area) in solid black. Maline Creek drains eastward through river-bottom woods into the Mississippi River, while to the west Coldwater Creek flows north into the Missouri. Wildwood is seen to lie between branches of Maline Creek, and consists of sloping land above cultivated bottoms to the east and south.

In 1817, shortly before the founding of the State of Missouri, extensive surveys were made of township and range lines in this area and details of topography and vegetation were recorded by the surveyors. From this material, preserved in the St. Louis County Engineer's office, it was possible to prepare fig. 1, which shows the distribution of forested and prairie land at that time. Hickories and Blackjack Oaks seemed to be the predominant types of trees. There is a strong tendency for the timber to be confined largely to the dissected headwaters of Maline Creek, and Gingras Creek and the River Des Peres to the south and west.

The surveyor, as he progressed along the range line of Section 12 a few chains east of Wildwood made the following remark: "Land rolling, soil rich and good for farming, thickly covered with oak and hickory". (Section 12 is indicated on fig. 1.) Significantly, however, he stated that halfway along this section line he built a mound (for a marker) in a "prairie," presumably a grass area surrounded by woods. Along the north boundary of the section the notation, "Prairie, good soil, scattering blackjacks and hickories," was made. On the west border the

country was "Gently rolling, scattering timber, blackjacks and oaks". It is thus vividly demonstrated that Wildwood was at the edge of the prairie. This fact plays a significant part in the history of Wildwood's vegetation.

On fig. 1 there also appears a soil boundary line. This was taken from the soil survey of the county made in 1923 (Krusekopf). It represents the eastern-most limits (in the county) of the Tama silt loam, a rather well-developed prairie soil. To the east is what was then called the Memphis, a forest soil. Apparently those grasslands described by the old surveyors as being east and south of this soil boundary line had not been established for a long enough period to have their inevitable effect on the soil. The grass was invading land which inherently belonged to timber.

Fortunately, one of the early Government surveyors that worked in the region, a Mr. R. W. Wells, was interested in this prairie-forest problem. In his article (Wells, 1819) "On the origin of prairies," he made the following statement:

> ...the writer has seen, in the country between the Missouri and Mississippi, [precisely the area with which we are concerned] after unusually dry seasons, more than one hundred acres of woodland together converted [by fire] into prairie. And again, where the grass has been prevented from burning by accidental causes, or the prairie has been depastured by large herds of domestic cattle, it will assume, in a few years, the appearance of a young forest. Numerous proofs of this fact can be adduced but a few shall suffice. The vicinity of St. Louis and St. Charles affords instances. Both these beautiful places are situated on what are termed first and second bottoms, or flats—the former on the Mississippi, the latter on the Missouri; the second or upper bottoms, in both, are high plains that commence within a few hundred yards of the rivers, and extend back many miles; all the old French inhabitants will tell you, that the prairies formerly came immediately up to those places. Now the surrounding country for several miles is covered with a growth of trees of four or five inches diameter, near the towns where the burning first ceased, and gradually diminishing in size as you recede, until you at length gain the open prairies.

Nearly twenty years later another writer made observations which provide an interesting sequel to Mr. Wells' description. In his diary of a trip through the outskirts of St. Louis in 1836 Edmund Flagg has written:

> The face of the country is neither uniform nor broken, but undulates imperceptibly away, clothed in dense forests of blackjack oak, interspersed with thickets of the wild plum, the crabapple and the hazel. Thirty years ago the broad plain was a treeless, shrubless waste without a solitary farmhouse to break the monotony. But the annual fires were stopped, a young forest sprang into existence, delightful villas and country seats are now gleaming from the dark foliage in all directions.

It is difficult now for us to visualize our predecessors of 100 years ago living in a country of scrub oak, but such seems to have been the case. This change was not a uniform one, however. As Wells pointed out, it often began in the vicinity of settlements. It undoubtedly moved faster on some terraine than on others. That there was still considerable prairie left northwest of St. Louis at the time Flagg made his trip is shown by a letter which Evert A. Duyckinck wrote in 1837 in which he described a trip he made from St. Louis to Florissant:

> I must give you an early account of our yesterdays visit to the humorous little old town of Florissant situated in the midst of the flowers of the Prairie. . . . We were off before six o'clock. . . . We stopped on the rough edge of the Prairie which lies around the city where the scrub oak and marshy weeds ill set off by the thick fog gave us no im-

> pression of the beautiful flowers and plants that lay beyond us in the fields to give so pretty a name to little Florissant. Here we breakfasted. . . . and were away again in the field. The mist gradually rolled away . . . & I had my first view of the Prairie rolling away & broken into innumerable landscapes with its unfenced fields of flowers and trees. A smooth level road lays through the Prairie which is rarely enclosed by fences and as B remarked it was a ride through a garden or the private lane on a gentleman's estate. (McDermott, 1944)

WILDWOOD TODAY

Wildwood was once one of those unfenced fields of trees. Today it still persists, though it is fenced and surrounded by suburbs instead of by prairie. It is mature now, even over-mature as the large number of dead and fallen trees on the diagramatic representation of the woods in fig. 2 show. Nearly one fifth of the trees had died in 1946. At the present writing the number has greatly increased. It is predominantly an oak-hickory woods. A complete tree-by-tree survey of the entire 41.5 acres in 1946 showed that Pignut Hickory, Black and Shingle oaks made up 54 per cent of the total. Twenty-one other species made up the rest of the population (Table I). A glance at fig. 2 suggests the open quality of the woods and shows the cow trails that have resulted from years of

TABLE I

ANALYSIS OF WILDWOOD BY TREE SPECIES (INCLUDING DEAD TREES)

Species	Dead	Alive	Total	% of Total	Frequency (% of zones in which found)
Black Walnut *(Juglans nigra)*		4	4	.5	13
Mockernut Hickory *(Carya tomentosa)*		2	2	.3	6
Pignut Hickory *(Carya ovalis)*	17	82	99	12.4	100
Shagbark Hickory *(Carya ovata)*		1	1	.1	6
White Oak *(Quercus alba)*	1	15	16	2.1	25
Post Oak *(Quercus stellata)*		3	3	.4	13
Red Oak *(Quercus rubra)*		4	4	.5	25
Black Oak *(Quercus velutina)*	*	101	101	12.6	81
Black Jack *(Quercus marilandica)*	1	29	30	3.8	56
Shingle Oak *(Quercus imbricaria)*	35	197	232	29.1	100
White Elm *(Ulmus americana)*		35	35	4.4	31
Slippery Elm *(Ulmus rubra)*	3	36	39	4.9	50
Hackberry *(Celtis occidentalis)*		11	11	1.4	13
Red Mulberry *(Morus rubra)*		2	2	.3	13
Sassafras *(Sassafras albidum)*		61	61	7.6	63
Sycamore *(Platanus occidentalis)*		2	2	.3	13
Black Cherry *(Prunus serotina)*	1	2	3	.4	13
Black Locust *(Robinia Pseudo-Acacia)*		2	2	.3	13
Ailanthus *(Ailanthus altissima)*		2	2	.3	6
Sugar Maple *(Acer saccharum)*	3	8	11	1.4	13
Silver Maple *(Acer saccharinum)*		2	2	.3	13
Box-Elder *(Acer Negundo)*		3	3	.4	13
Gray Dogwood *(Cornus racemosa)*		2	2	.3	13
Persimmon *(Diospyros virginiana)*	2	72	74	9.3	6
Oak, dead, species unidentified	30		30	3.8	63
Unidentified dead trees	26		26	3.3	63
TOTAL	119	678	797		

* Included under dead oaks, below.

grazing. To locate particular areas and to get an idea as to which species were most widely distributed, the wood-lot was roughly divided into 16 zones by superimposing a grid. Table I shows the calculated frequency of the different species. Shingle Oak and Pignut Hickory occurred in all zones and Black Oak in all but three. Persimmon and Sassafras were the next most abundant trees though only the Sassafras was widely distributed, most of the persimmons being in a single copse.

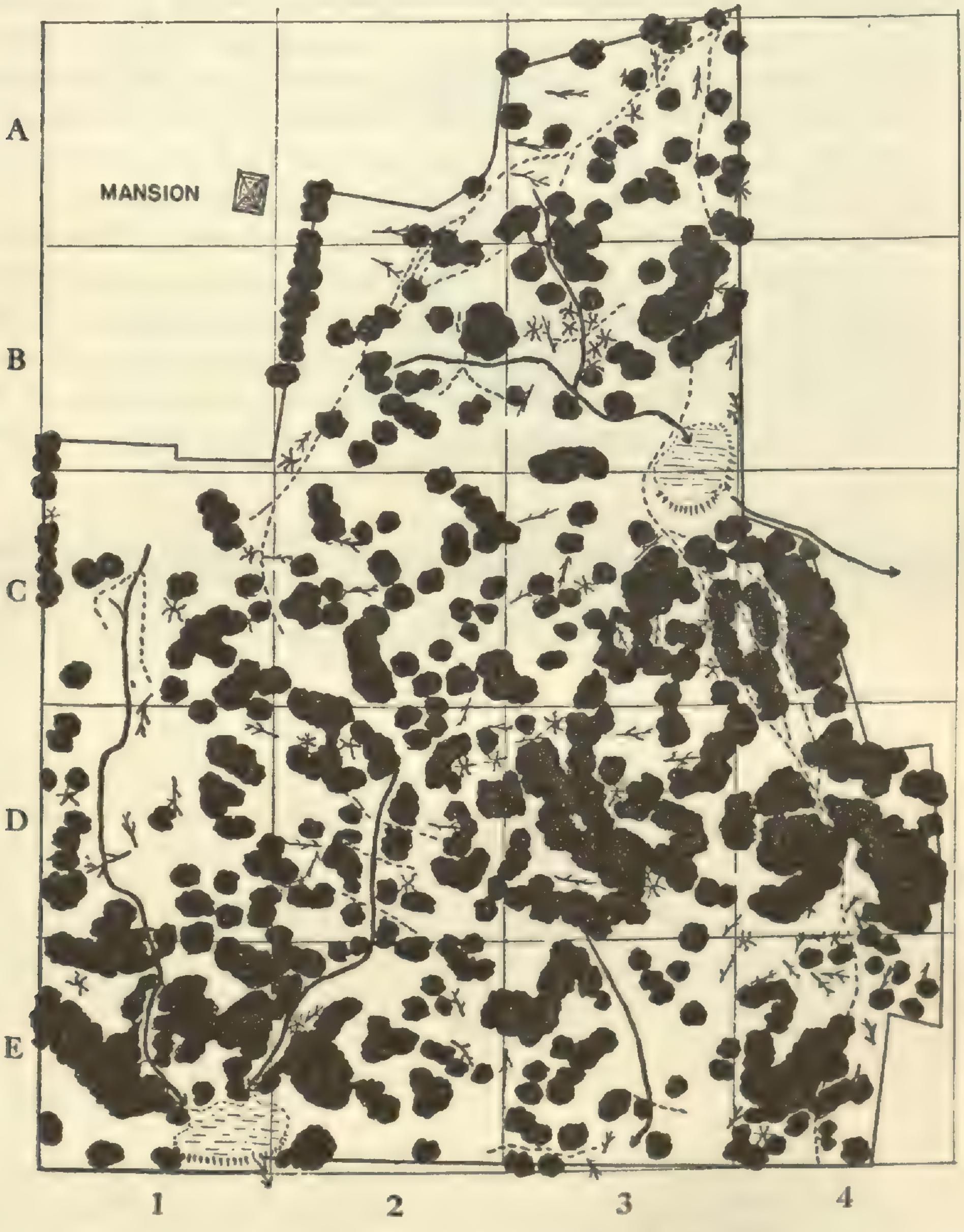

Fig. 2. Diagrammatic representation of Wildwood.

Solid black—Live trees
Radiating branches—Standing dead trees
Prone trunks—Fallen trees
Solid lines—Drainage
Dotted Lines—Cow paths
Hatchures—Dams
Horizontal and vertical lines divide Wildwood into zones

AGES AND THE PAST

In order to learn in more detail what Wildwood's role may have been in the transition from prairie to forest and to attempt to find out what influence successive phases of exploitation may have had, an intensive study was made of the ages of the trees in the woods. In some cases ages were obtained by simple stump counts, but ordinarily the procedure used was as follows: With an increment borer a core was procured from the desired tree, but since the borer available was only 10 inches long, it was only in smaller trees that ages could be read direct. Ordinarily it was necessary to procure cores and stump counts from a number of different sizes of trees of a given variety. Measurements of growth in years per inch were then made and averaged to reduce the error due to skewed boring, tree shape and diameter, and habit of growth. An index in years per inch was thus obtained for 16 different tree species (Table II). The circumferences of 222 trees selected at random in all parts of the woods were then taken. These circumferences were converted to diameters and ages, according to the calculated growth index for the species. These ages were then tabulated as averages of successive twenty-year periods taken every five years. These averages were adjusted so that they represented each species in proportion to the number of individuals of that species in the total woods population in 1946. The resulting graphs are shown in figs 3 and 4.

TABLE II

DIAMETERS, HEIGHTS, AND GROWTH RATES OF TREE SPECIES WITHIN WILDWOOD

Species	Ave. diam. breast high (inches)	Ave. height (feet)	H/D (feet)	Rate of growth in yrs. per in.		Ave. age allowing 1-inch bark for all species	Diam. smallest tree (inches)	Age smallest tree (years)	Diam. largest tree (inches)	Approx. age largest tree (years)
				Last inch	Entire tree excl. bark					
*BlackWalnut *(Juglans nigra)*	18	47	32				11		25	
Hickory *(Carya* sp.)	19	69	44	8.5	7.0	126	12	77	32	217
White Oak *(Quercus alba)*	27	82	37	3.3	4.2	109	9	34	37	151
*Post Oak *(Quercus stellata)*	15	53	43				11		27	
*Red Oak *(Quercus rubra)*				5.5	4.1				46	185
Black Oak *(Quercus velutina)*	31	83	32	6.6	4.8	144	18	82	46	216
Black Jack *(Quercus marilandica)*	26	56	26	8.5	5.6	140	16	84	44	240
Shingle Oak *(Quercus imbricaria)*	26	76	35	8.2	4.7	118	12	52	42	193
White Elm *(Ulmus americana)*	23	66	34	2.1	2.1	46	13	25	41	84
Slippery Elm *(Ulmus rubra)*	19	61	39	6.5	5.0	90	9	40	29	140
Hackberry *(Celtis occidentalis)*	15	42	34	5.5	3.8	53	10	34	19	68
Sassafras *(Sassafras albidum)*	24	48	24	6.	4.8	110	8	34	42	197
*Sycamore *(Platanus occidentalis)*	27	85	38	2.0	1.8	47	22	38	33	58
*Black Cherry *(Prunus serotina)*	22	71	39	10.5	5.4	114	14	69	29	151
*Ailanthus *(Ailanthus altissima)*	21	42	24	2.5	1.7	34	17	27	25	41
Sugar Maple *(Acer saccharum)*	14	48	41	7.3	5.5	72	9	44	29	154
*Silver Maple *(Acer saccharinum)*	25	87	42				19		31	
*Box-Elder *(Acer Negundo)*	21	55	31	7	5.6	112	17	90	24	129
Persimmon *(Diospyros virginiana)*	14	57	49	9.7	4.5	58	9	36	24	104
All Species	22	66	36	6.2	4.4	92	8		46	

* Numbers very limited

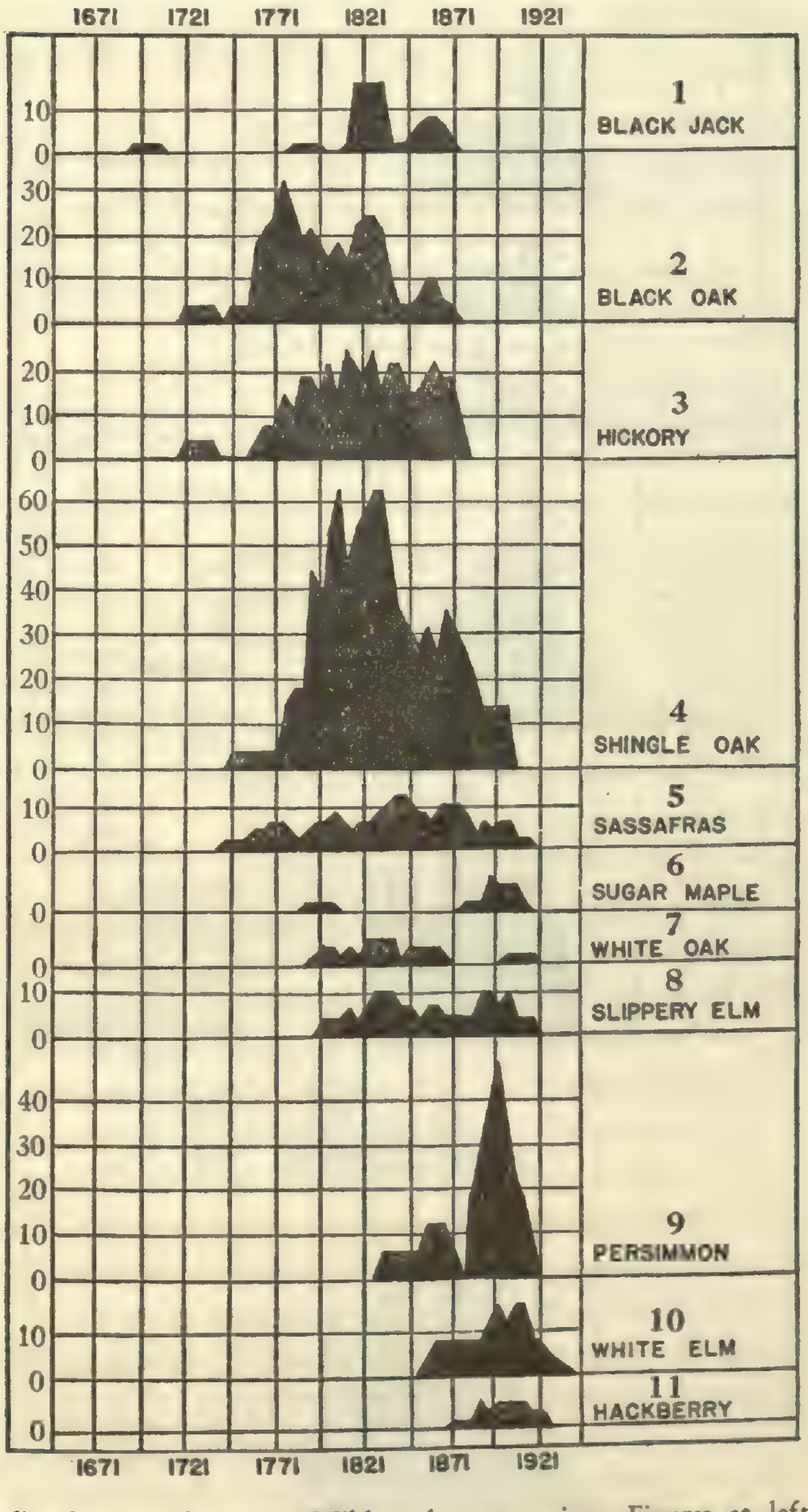

Fig. 3. Age distribution of various Wildwood tree species. Figures at left are numbers of individuals.

It seemed a reasonable possibility that graphs similar to those obtained from present-day Wildwood might be calculated for the witness trees used in old surveys, since diameters and species are given. Three surveys had been made in the area of the original Spanish grant, or on adjacent section lines at convenient times in the past: the original survey of 1818, and two subsequent ones in 1850 and 1871. They included a few areas as much as a half mile from Wildwood, but it is felt that conditions are sufficiently uniform for them to be useful. The numbers

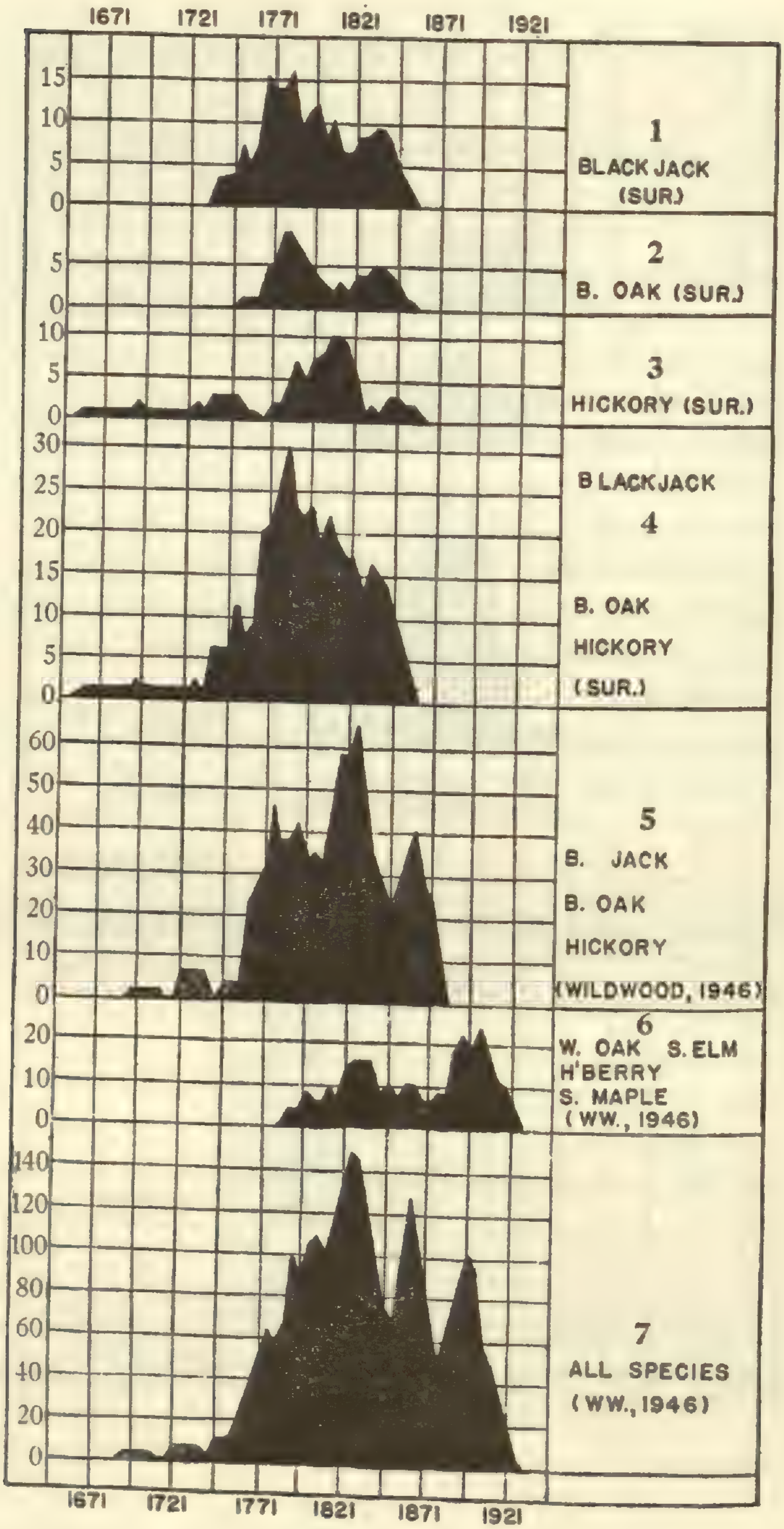

Fig. 4. Age distribution of trees of various species found in Wildwood, or listed as witness trees in surveys of 1821, 1850, and 1871. Figures at left are numbers of individuals.

and diameters of different species of witness trees are compared with the trees of the study area in Table III. By using the growth index for each species as calculated earlier, the ages of the survey trees were compiled, and all adjusted to date from 1946. A total of 99 trees was thus involved in the composite graph (fig. 4,

TABLE III

COMPARISON OF WITNESS TREE DATA WITH PRESENT DATA

Species	Year of survey: 1818 Numb. of trees	1818 % of total	1818 Ave. diam. (inches)	1850 Numb. of trees	1850 % of total	1850 Ave. diam. (inches)	1871 Numb. of trees	1871 % of total	1871 Ave. diam. (inches)	1946* Numb. of trees	1946* % of total	1946* Ave. diam. (inches)
Hickory *(Carya* sp.)	4	12	14	14	35.	12	11	23.	10	80	11.9	19
White Oak *(Quercus alba)*							2	4.	15	15	2.2	27
Post Oak *(Quercus stellata)*							1	2.	18	3	.4	15
Red Oak *(Quercus rubra)*	3	9	6				4	8.	15	4	.6	
Pin Oak *(Quercus palustris)*							6	13.	11			
Black Oak *(Quercus velutina)*	6	18	9	4	10.	5	11	23.	16	101	15.	31
Black Jack *(Quercus marilandica)*	20	61	9	21	53.	9	8	17.	13	27	4.	26
Sassafras *(Sassafras albidum)*							1	2.	7	53	7.9	24
Sycamore *(Platanus occidentalis)*				1	2.5	18				2	.3	28
Wild Cherry *(Prunus serotina)*							2	4.	12	2	.3	22
Cottonwood *(Populus deltoides)*							1	2.	18			
Total	33			40			47			287		
Number of species		4			4			10			24	
Ave. diam., all trees			10			9			12			24

* Only those trees are included in this column for which comparisons are available. All hickories are totalled together, since no differentiation was made in the survey.

No. 4) of the three species for which there were sufficient data. Separate graphs of the three species are given in fig. 4, Nos. 1, 2, and 3.

Considering the many possibilities of error in the application of such average growth indices and the heterogeneity of the data, the results are more than interesting. In fig. 4, No. 4 is the compilation of tree-age data from survey sources. Numbers 5 and 7 are summaries of Wildwood growth. These curves strongly suggest an abrupt increase in tree sprouting some time between 1745 and 1780. If only the last curve were available, it would be easy enough to attribute this rise merely to the longevity of the species involved, but the trees of the survey were measured as early as 1817, and at two subsequent intervals. Yet the curve begins to rise at the same place. Also, the fact that the curves are based on a composite of species is further evidence that it is not mere maturity which accounts for the sudden rise, for the maturity of species so diverse as hickory, Black Oak, and Blackjack would not be expected to coincide. The case is pretty strong for a rather abrupt increase in the sprouting of these species.

Previous to the 1745-1780 increase the data available strongly suggest a condition such as the surveyors describe as "scattered blackjacks and hickories." Where these early trees came from and whether they were invaders in an unstable prairie or remnants of an older forest, it is impossible to say. The broad open aspect of the oldest trees still alive and the reputation of blackjacks and hickories as invaders of cut-over and burned areas would suggest that they were the only

elements of the tree flora which were capable of maintaining themselves under prevailing conditions. Old climax growths of Sugar Maple, Basswood, Hackberry, or White Oak, if they ever existed, have been largely destroyed by fires, although a single Sugar Maple, completely hollow and fire scarred, must date back to 1800, and possibly even to 1750. This tree was on a moist northeast slope. In all probability islands of climax woods existed in moist protected areas, just as they seem to have done on some Wisconsin sites (Ellarson, 1949). Constant infection of prairies with seedlings and sprouts and constant scorching of wooded islands by fire were the order of the day. The balance was upset by forces operating in the last half of the eighteenth century. Is it mere coincidence that St. Louis was established in 1764, Florissant in 1785, Creve Coeur (a few miles west) in 1793? These early settlements were not made without disrupting the prevailing Indian population and consequently the firing practices described by Wells and Flagg. Even fires started by the white settlers or by natural causes would have been restricted by developing roads, crop land, timber clearing, the activities of domesticated animals, and hay cutting.

The composite curve of all species in Wildwood (fig. 4, No. 7) shows that the peak of tree invasion occurred about 1825, shortly after Missouri had become a state, and Mullanphy had taken over the property of Wildwood. This peak was largely the result of the intrusion of a large number of Shingle Oaks between 1800 and 1825. Apparently the grass had been sufficiently weakened and the proper amount of hazel and dogwood had grown up to permit the successful establishment of the Shingle Oak.

It is interesting that so-called virgin timber is a rare thing in much of the Middle West. Instead, there are remnants of these extensive oak forests which came in after the fires stopped. Such growths are seen in other states, especially Wisconsin and Iowa. In Wisconsin, however, the average age of these stands runs much closer to 105 or 110 years than 135. It is probably no coincidence that the rush of settlement to Wisconsin did not occur until about 1840 or so. In western Iowa even-aged stands of oaks which have come into the prairies are only some 80–90 years old. Western Iowa had a population of less than two people per square mile until 1855.

This relatively sudden disappearance of prairie land before the forests is sometimes attributed to climatic changes, but it is hardly likely that climatic change would have manifested itself so suddenly and so coincidentally with the white man's progress across the country. It is probable, however, that a climatic change of low intensity but of broad distribution had already occurred some time in the past, and had left the prairie-forest border in tension that could be easily upset by changed land use.

It is of some interest that by the time a peak of new forest growth had been reached, slightly more mesophytic types began to make noticeable progress through the woods. This is especially true of White Oaks and Slippery Elms (fig. 3, Nos. 7 and 8). Following the peak of 1825, new tree growth dropped to a low level

in 1850. We can only guess that this was associated with the heavy competition of the developing forest, or possibly it was related to some agricultural activity of a minor sort carried on by Mullanphy's tenants.

By 1865 a new surge of growth is evidenced in oak, hickory, persimmon, and sassafras. The Civil War was a period of considerable readjustment for society in general and particularly for that founded on slavery. We might surmise that Major LaMotte found it especially difficult to maintain his herds and other activities at Wildwood while the conflict was on, with the result that a new forest began to develop. Doubtless such an effect of the war would be evident over rather wide areas, and study on a more extensive scale might show it to have been general.

Following the war Major LaMotte's activity began in earnest. The decline of tree growth shown on the graph is undoubtedly associated with the increase of his herds. It may be significant also that by 1870 a railroad had been built just south of the woods, and fires probably caused some destruction to young trees. The tenant farmer, now nearly ninety and a resident of the area for some seventy years, recalled several serious fires started in this manner.

Major LaMotte died in 1892. By 1896 Wildwood had begun to be a tangle of new sprouts, this time of Persimmon, Sassafras, Hackberry, Sugar Maple, White Elm and Slippery Elm (fig. 4, No. 6). These trees were largely in the more moist parts of the woods, where seedlings could reproduce. Apparently conditions had progressed to the point where establishment of oak and hickory was not successful. In 1920, the advent of Mr. S——'s dairy changed the picture again. Cows and brush-cutting and burning put a complete stop to Wildwood's investment in future wood.

DENSITY OF WOODS

As another approach toward reconstruction of earlier conditions in Wildwood and vicinity, the density of the woods was considered. In 1946 there were 797 trees, dead and alive, on 41.5 acres—an average of 19 per acre. Although some trees have fallen and been chopped for kindling, split for fence-posts and burned to clear the pasture, it can well be seen that this woods was never at any time a fully-developed forest, or even-aged stand of hardwoods, for under such conditions Schnur (1937) indicates that in a stand averaging 100 years of age on an excellent site one might expect close to 150 trees per acre. This figure is obtained under ideal conditions of sprouting and unhampered growth. Wildwood has been pastured off and on for almost 100 years so that its normal cycle of reproduction could never have been achieved.

From a sample measurement of about one tenth of all the trees in the woods an average horizontal spread of 43 feet or about 1450 square feet was obtained. If the latter figure is multiplied by 797, a total acreage of 26.6 acres is shown to be directly beneath trees or occupied by fallen ones (the average fallen tree was found to cover an amount of ground practically equal to that of the living ones), leaving 14.9 acres of open pasture, which is fairly evenly distributed about the

woods (fig. 2). If all the 797 trees were evenly spaced within the area they would be about 55 feet apart. Of course, no such ideal spacing occurs. Along the east border the density is as high as 50 trees per acre while in the northwest portion the density drops to 11. The majority of the woods, however, has a density close to the average of 19.2 trees per acre.

It is interesting to compare this density to densities of the past woodland as indicated by data from the three early surveys already mentioned. Table IV shows the average distances and angles between witness trees from the surveyor's station. It was common practice to take trees as close to the section corner or survey marker as possible; in any case trees beyond 100 feet are not desirable. Within very broad limits, therefore, an average of the distances will be roughly indicative of the density of the woodland. In the same way an angle between two trees should be close to 90 degrees. The denser the woods the more choice the surveyor would have and a higher percentage of angles close to 90 degress would be expected. It is advisable also to take trees of fair size which are well established and give promise of long life. These data are not nearly as extensive as might be desirable, and it must be remembered that the conscientiousness of the surveyor and numerous other factors might affect the results. It is felt, however, that such figures, if properly pursued and compiled, could be used to indicate the condition of woodlands of the past over considerable areas.

The average tree of 1946 is much larger than that of any previous period. This is exaggerated by the present absence of small growth due to continual grazing. It is evident, however, that there are many trees in the woods which are larger than the largest tree during any other period. The average distance between trees, or from an arbitrary spot to the witness tree, compares closely in 1946,

TABLE IV

COMPARISONS INDICATIVE OF DENSITY OF WOODS IN VICINITY OF, OR IN, WILDWOOD DURING VARIOUS YEARS*

Year	Number of species	Number of trees	Diam. smallest tree (inches)	Diam. largest tree (inches)	Diam. average tree (inches)	Av. dist. of Witness tree (feet)	Angle between witness trees		
							% between 70° & 110°	% between 40° & 140°	% between 20° & 160°
1818	4	33	4	18	10	58	25	33	67
1850	4	40	2	28	9	74	21	63	68
1871	10	47	4	24	12	60	25	65	90
1946	24	287	8	46	24	55†			

* Data for 1818, 1850, and 1871 based on witness trees recorded in old property surveys.
† Average distance between trees if they were equally spaced over total area.

1871, and 1818. The survey in 1850 took smaller trees and larger trees than either of the other two surveys, had a smaller average tree size, and had a larger average distance between trees, suggesting that in the areas surveyed the trees were somewhat sparser. In the angles between witness trees there is no suggestion that the woodlands were sparser in 1850. In 1871 conditions would seem to have been closest to those of the present, with a greater variety of species, a larger average diameter, and a witness-tree distance similar to the distance between trees at present. The angle data also suggest a greater degree of selectivity than at any other period. One might expect the woods to be sparser now due to the death and disappearance of trees, and this might be true but for a brief intermission in grazing which permitted the sprouting of certain trees. Actually, however, there is little evidence that very many trees have died until just recently.

RATES OF GROWTH

The rates of growth (Table II) of the various tree species are all greater than are usual, showing that the soil and location are excellent. A White Oak 37 inches in diameter, from the average Missouri site, might be twice the age of the one in this woods which is 100 years old. The wide spacing of the trees in Wildwood would also encourage rapid growth. In most cases the last inch of growth has been very slow, especially in the Blackjacks, Shingle Oaks and Persimmons. This is probably due to a combination of factors, including the maturity of the trees, the competition of the grass sod, and perhaps even the establishment of a match factory nearby, from which strong fumes of sulphur commonly invade the woods.

The fastest-growing tree is *Ailanthus*, with an average of 1.7 years per inch. This is essentially a fence-line tree and is not an integral part of the wood-lot, though many show considerable promise of establishing themselves before long, for they are the only young trees which can withstand the nibbling of cows and horses. Sycamores with 1.8 and White Elms with 2.1 years per inch grow almost as fast. None of these trees predominates in the woods. The slowest growing tree is the hickory, with an average of 7 years per inch.

UNDER THE TREES

Upon entering the woods from the west one crosses a stile over a barbed wire fence. Through the overhanging branches of sassafras that line the fence one can see a broad pasture which in spring may be plain bright green, or dotted with yellow dandelions. In late summer it is clouded with the white bloom of boneset. In winter the scattered stems of weeds fall and the sod slowly loses its greenness.

Beyond this open pasture the trees begin: a hickory, a group of Shingle Oaks, irregular ranks of trees along the gullies extending toward the ridge. In the sun-filled patches between trees there are usually old stumps, or whole fallen trees which gather about them, in late summer, canopies of pokeberries. Great trees that die drop bark and twigs and change the sod beneath to a collection of weeds, including pennyroyal *(Hedeoma pulegioides)*, Three-seeded Mercury *(Acalypha vir-*

ginica) and Horse-Nettle *(Solanum carolinense)*. In the deep shade of Sugar Maples the ground remains bare except in spring when Aunt Lucy *(Elissia nyctelea)* and Spring Beauty *(Claytonia virginica)* take the brief opportunity to bloom and seed. In the low shade about the pond violets and smartweed *(Polygonum Hydropiper)* and Fog Fruit *(Lippia lanceolata)* almost exclude the bluegrass.

Most of the plants of the woods survive only because they are unpalatable to cows, or, like violets and buttercups, get a good start in spring before the pasturage is sufficient to permit grazing. Even though the cows are in the woods by April, plants with persistent underground rhizomes or bulbs such as May-apple *(Podophyllum peltatum)*, Green Dragon *(Arisaema Dracontium)*, *Viola* sp., Violet Wood-sorrel *(Oxalis violacea)*, and Yellow Star-Grass *(Hypoxis hirsuta)* flourish. Dwarf Larkspur *(Delphinium tricorne)*, Indian Tobacco *(Lobelia inflata)*, White Snakeroot *(Eupatorium rugosum)* and similar poisonous species appear here and there, but are avoided by the cows. In July, catnip *(Nepeta Cataria)*, Mountain Mint *(Pycnanthemum virginianum)* Hedge Mustard *(Sisymbrium officinale)*, smartweed *(Polygonum Hydropiper)*, and the nettles *(Urtica* sp.) appear in patches. Species that sprinkle the open pastures, such as milfoil *(Achillea Millefolium)*, Bull Thistle *(Cirsium vulgare)*, ironweed *(Vernonia* sp.), mullein *(Verbascum Thapsus)*, and fleabane *(Erigeron* sp.) bloom at various times during the season, but none rival the great surge of boneset *(Eupatorium serotinum)* in late summer.

There is little suggestion in the flora of any prairie influence and there are remarkable few true woodland plants (Appendix I). In a few relatively stable places beside fallen trees *Arisaema Dracontium* may appear, but no *A. triphyllum.* In the same place may be American Bell-flower *(Campanula americana)*. In a protected corner is a single clump of Sensitive Ferns *(Onoclea sensibilis)*. In the open pasture one may find in earliest spring bluets *(Houstonia minima)* and field pansies *(Viola Kitaibeliana)*. About the fences are patches of Spider Flowers *(Cleome spinosa)* and hemp *(Cannabis sativa)*. Thick clumps of Blue Mist flowers *(Eupatorium coelestinum)* and common balm *(Melissa officinalis)* are found in openings in the woods; in the wet places are Monkey Flowers *(Mimulus ringens)*, spearmint *(Mentha spicata)*, and the big Blue Lobelia *(Lobelia spicata)*.

Beneath these gaunt trees there is no distinguished company of plants. There are familiar weeds of both native and foreign origin, and some common wild flowers of intermediate habitats. Combined with Kentucky bluegrass they provide the typical understory for a pastured woods, or wooded pasture, whichever we may prefer to call Wildwood. While its flora is undistinguished, it is a complex dynamic environment. No balance exists as it does in open pasture or prairie or in a climax forest. Not only is there the subtle struggle between trees and grass, between weeds and grass, but there is the vigorous, daily-witnessed, positive destruction of plants and plant habitats by cows, by falling trees and branches, and by man's varied ingenuity. In many environments from day to day one can scarcely discern any changes beyond those inflicted by unusual weather conditions,

or the normal progression of the seasons. In Wildwood there is seldom a day that passes that there is not some visible alteration. One day the woods is burned, on another a fallen Shingle Oak is split for fence-posts, campfires are built, mushroom hunters collect a crop of fungi in the morning mist, squirrels are shot, cows push soil into the creek, the ponds dry up—everything is changing. It is an environment where weeds find many opportunities for establishment. The following list suggests some of them:

Livestock.—
- Patches of dung
- Hoofmarks in loose wet or thin sod
- Paths
- Closely grazed spots where grass is pulled up by roots
- Broken banks along streams

Man's activities.—
- Bare areas from which sod has been cut
- Disturbed soil where fence-posts are split
- Dumps of trash, ashes, and garbage
- Fence lines
- Tractor trails
- Campfire areas
- Burned litter and leaves
- Broken dams and drained ponds

Weed patches.—
- Weakened sod or bare soil next to rank weed growth

Fallen trees.—
- Rotten wood
- Sod killed by shade and changed soil composition
- Disturbed soil caused by fall of tree
- Upturned roots

Rainfall.—
- Deposits of eroded soil on grass
- Concentrations of litter caused by heavy rains
- Gullies washed free of leaves by heavy rains
- Bare areas of soil caused by standing water

Miscellaneous.—
- Ant hills
- Gopher hills
- Dung beetle diggings
- Dog scratchings at bases of trees
- Sour soil beside tree trunks

FLOWERING PERIODS

In an effort to arrive at some quantitative expression of the flora, phenological records were kept on the week of first bloom and peak of bloom of 70 species during the year 1946. The graphs of these data are shown in fig 5, Nos. 1 and 3, and are prepared by using the number of species beginning bloom or in peak of bloom during successive 24-day intervals. By way of comparison, curves translated from Anderson and Hubricht (1940) are given in fig. 5, Nos. 2 and 4. These are from composite data on several habitats in an area some 30 miles southwest of Wildwood. First-bloom data give a curve very similar in its major aspects to that for the peak-of-bloom, though the peaks are naturally earlier. Since first-bloom is less subject to personal judgment than peak-of-flowering it would seem that in many cases the former alone would suffice.

Graphs of flowering peaks of two habitats, woodland and meadow, copied from the above-cited work are here reproduced in fig. 5, Nos. 5 and 6. The graph for Wildwood bloom is seen to contain a suggestion of both these graphs with a somewhat subdued spring bloom and a strong late summer flowering. Undoubtedly many aspects of the history and environment of the flora are combined in these curves. One might consider such curves as floral spectra, capable of expressing

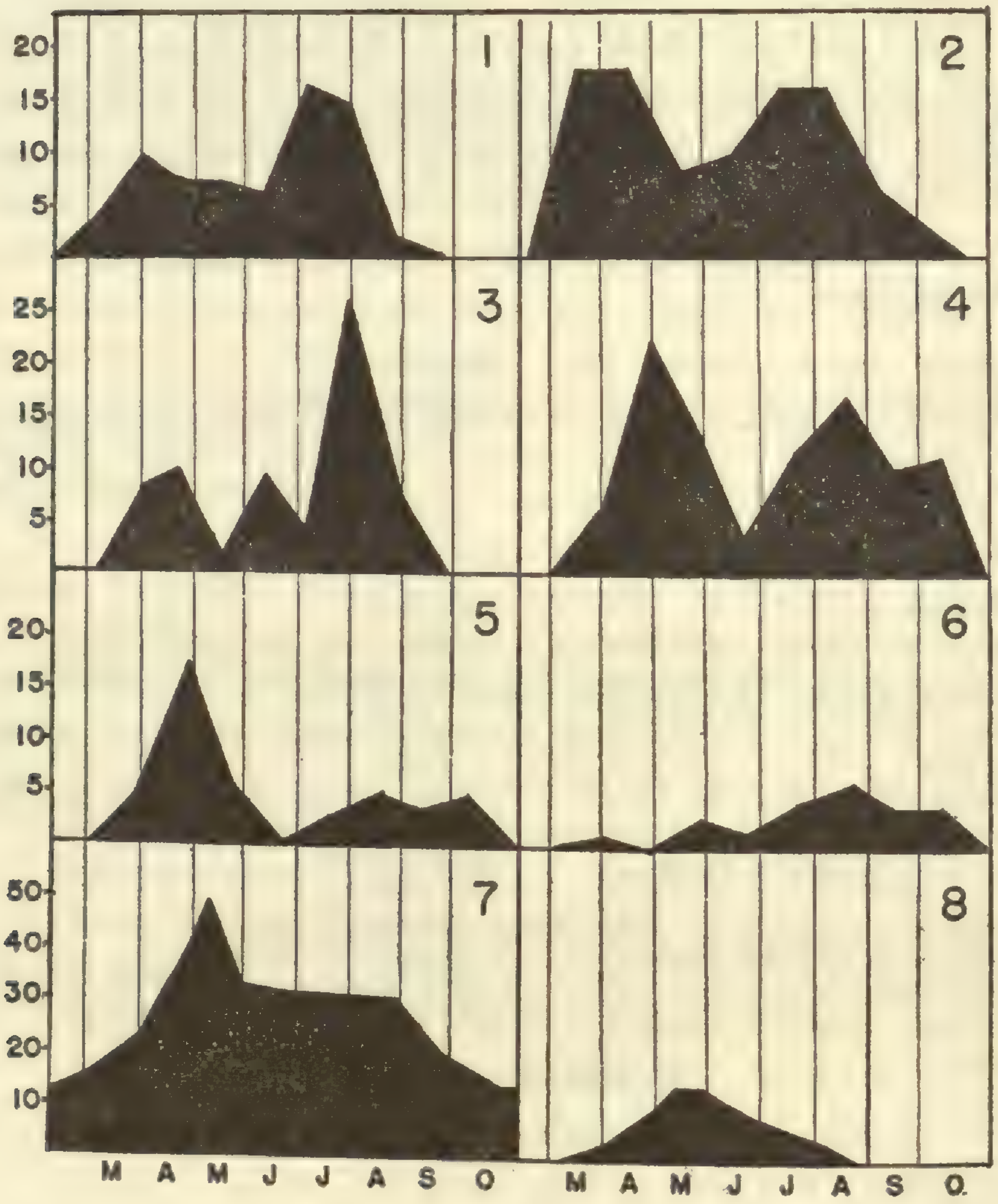

Fig. 5. Phenological graph of flowering, bird population, and nesting birds. Vertical figures, number of species; horizontal letters, months beginning with March.
No. 1—First bloom of 70 flower species in Wildwood.
No. 2—First bloom of 96 flower species compiled from data in Anderson and Hubricht (1940).
No. 3—Peak of bloom of 70 flower species in Wildwood.
No. 4—Peak of bloom of 96 flower species from graph in Anderson and Hubricht.
No. 5—Peak of bloom of woodland species from Anderson and Hubricht.
No. 6—Peak of bloom of 23 meadow species from Anderson and Hubricht.
No. 7—Number of species of birds in Wildwood during spring and summer, 1946. (Data for the fall migrations were not obtained. Winter population included 12 species.)
No. 8—Number of species nesting in Wildwood during summer, 1946.

the characteristics of an environment somewhat as absorption bands of the spectroscope express the chacteristics of a compound. Were enough accurate complete phenological data on restricted areas available, much valuable information concerning the organization of environments might become available, especially with reference to processes integrating plant and animal activities, and processes activating plant and animal growth and reproduction.

GROUND COVER

In the low southwest corner of Wildwood a survey of the plant population was made by estimating the proportion of ground covered by different species within the horizontal spread of sample trees. In Table V the results are tabulated by plant and tree species. The frequency and degree of dominance of each plant were calculated. Plant communities were not divided into different horizons, for tall weeds were not conspicuous. The figures are based on a hasty estimate of total plant coverage, not on basal area or number of individual plants. This was found to be a fairly satisfactory method for arriving at a rough mathematical conception of the vegetation. Bluegrass composed 29 per cent of the total. This is the only plant in the entire collection which provided any satisfactory stock food. Nimble Will *(Muhlenbergia Schreberi)* provided a random mouthful as did a few other grass species. The tips of smartweed were grazed carefully; tree seedlings and clover, though readily eaten, were very scarce. Plantain was eaten in early spring and blackberry leaves were eaten any time.

The sheer waste and inefficiency of pastured woods is made strikingly evident. Not more than 35 per cent of the entire vegetation in shaded areas is edible, and even that is of low feed value. No estimate of coverage was made in unshaded areas, but even assuming 90 per cent available pasturage (which is very generous) the total available pasturage throughout the 41.5 acres of Wildwood amounts to 22.7 acres or little more than one-half the total area. This leaves an average of one-half acre for each of the farmer's 43 head of stock during the grazing season. Little wonder he has to feed his cows heavily all year long. It is little wonder also that gullies and weeds grow faster than the grass, for hungry cows search the banks of creeks for grass and push the soil and sod into the path of washing water. They graze closely and walk unnecessary distances in search of food. The strain is more than thin sod can stand.

ANIMALS

Man's activities determine with the same consistency the nature of the animal community, for intensive grazing in a woodland discourages at least two-thirds of the normal population of wild life. The whole mid-section of the forest is removed and a void is left in which only occasional visitants play an active part. There are plenty of moles throughout the shaded part of the woods. In the full sun of the pasture along the fence-lines Pocket Gophers establish their mines. Short-tailed Shrews navigate beneath scattered leaves and logs. White-footed Mice keep their nocturnal appointments throughout the woods. Only two or three pairs of Cottontail Rabbits were seen within the limits of Wildwood, and these were near the fence lines. Chicken, Garter, and Black Snakes, toads, Box Turtles, and Painted Terrapins were sometimes seen, but none was common.

The lack of permanent cover is of the greatest importance in the life of these ground species. One might expect that the wealth of fallen trees would present an ideal arrangement for a variety of animals, but fallen trees disappear almost as if by magic beneath the devices of horns, hooves, and calloused tongues, aided by

TABLE V

ANALYSIS OF VEGETATION BENEATH 32 TREES
(AVERAGE HORIZONTAL SPREAD 43 FEET)

Species	Frequency of occurrence		Per cent of total area occupied
	Numb. trees under which found	Per cent	
Bromus secalinus	3	9	.4
Poa pratensis	30	94	29.2
Hordeum pusillum	1	3	
Agrostis perennans	5	16	2.4
Muhlenbergia Schreberi	27	88	16.6
Digitaria sanguinalis	4	13	.2
Setaria glauca	2	6	
Arisaema Dracontium	1	3	
Commelina communis	4	13	
Juncus tenuis	5	16	.4
Quercus (seedlings)	3	9	
Ulmus (seedlings)	14	44	.2
Morus rubra (seedlings)	6	19	
Urtica procera	2	6	1.0
Rumex Acetosella	5	16	.6
Polygonum Hydropiper	31	97	27.6
Chenopodium ambrosioides	3	9	
Phytolacca americana	19	59	4.1
Sassafras (sprouts)	2	6	
Lepidium virginicum	6	19	
Sisymbrium officinale	2	6	
Rubus sp.	3	9	
Trifolium repens	11	34	1.9
Oxalis europaea	6	19	.2
Acalypha ostryaefolia	5	16	.5
Rhus radicans	4	13	
Viola papilionacea	14	44	4.7
Sanicula canadensis	1	3	
Osmorhiza longistylis	1	3	
Diospyros virginiana	1	3	
Verbena urticifolia	9	28	.2
Lippia lanceolata	3	9	.1
Teucrium canadense	4	13	
Nepeta Cataria	1	3	
Glechoma hederacea	2	6	.4
Prunella vulgaris	2	6	
Hedeoma pulegioides	5	16	5
Melissa officinalis	1	3	
Mentha spicata	2	6	
Solanum carolinense	14	44	.5
Physalis pumila	3	9	
Verbascum Blattaria	1	3	
Verbascum Thapsus	1	3	
Scrophularia marilandica	4	13	
Plantago major	9	28	.5
Sambucus canadensis	10	31	
Lobelia inflata	1	3	
Vernonia altissima	2	6	
Eupatorium serotinum	31	97	6.2
Erigeron annuus	1	3	
Gnaphalium purpureum	3	9	.2
Ambrosia trifida	11	34	.4
Ambrosia artemisiifolia	2	6	
Cirsium vulgare	2	6	.2
Taraxacum officinale var. *palustre*	6	19	.4
Bare ground	4	13	1.2

molds and fungi. The average fallen tree is a coarse skeleton the first year. With the accumulation of leaves about the limbs fire destroys them rapidly. The trunk may linger much longer, harboring a succession of mold and insect life until the slow digestion of the log returns to the soil material borrowed a century before.

The empty lower elevations of the wood are seldom occupied unless it be by some brief gambol of a squirrel or by night a flying squirrel. Both Fox Squirrels and Gray Squirrels are found in quantity on the ground when nuts, acorns, or maple squirts are ripe. The rest of the time they are lost among the high branches or in hollow-tree dens. While surveying bird nests I had intended to estimate the number of den trees available in the woods, but the number of dens was soon found to exceed any possible demand. On the first of June and the next few days following, a total of 22 semi-permanent type leaf nests used for summer litters were counted, two of which were in old crows nests (fig. 6).

The squirrel-hunting season opened on May 30, and in the week following 41 squirrels were shot, and among those examined 18 were Fox and 16 were Gray Squirrels. The majority were young of the late winter breeding. After the first week very few squirrels were shot. The inexperienced young were decimated or educated and the older squirrels had retired to secret places for purposes closely related to the further propagation of the race. Many of the squirrels killed were on their way to and from mulberry trees. A majority were taken from the heights of oaks, in true Missouri style, with rifles, though shotguns and air-guns were also used. Since Wildwood is so surrounded by suburban developments the hunting pressure is extreme, and because of its small size and isolation it is not protected by wardens. The squirrels shot in the first week averaged one per acre. There could not have been less than two squirrels per acre at this time, and that is allowing a 50 per cent kill, which, though possible, probably is excessive even under great pressure. The ratio of Fox Squirrels to Gray Squirrels seemed to be about one to one. There was general agreement among the hunters that the Fox Squirrels were a relatively recent addition to the woods population. Two Black or Swamp Gray Squirrels were seen near a copse of persimmons, and a melanistic Fox Squirrel came regularly to the mulberry tree.

On moonlight nights a few perambulating opossums, in spite of their hoary camouflage, were easily discernible. Their droppings of persimmon seeds were occasionally found, suggesting how the isolated persimmon trees came to be scattered about the woods. No raccoons were discovered, although in the lower areas along Maline Creek their tracks were common. A Red Fox was occasionally seen, but he too came from the vicinity of the creek. The house cat was the dominant predator of the woods. Cats were the most frequent victims of a mammal trap I set for other animals. There were few days that one was not seen stalking grasshoppers, sparrows, or mice along the fence rows.

BIRDS

To the average person strolling through Wildwood the only wild life discernible consists of a few scattering birds. Few people would imagine that at least 84 different species could be seen within this small, seemingly uniform environment (Appendix II). In early May, a total of 49 different species were seen in a single morning. This is unusual, for the summer population would not consist of more than 31 species, of which only 21 actually nest in the woods. The number of species active during the months of February to October are graphed in fig. 5, No. 7. Nest activity is shown in fig. 5, No. 8.

In winter there are ordinarily 12 species of birds in the woods. Strangely, this number does not include the Chicadee and White-breasted Nuthatch. Something they need is missing. Nor does it now include the Great Horned Owl, which must have been there in the past. Only the Screech Owl remains to represent the Strigidae. Of the winter residents only a few are truly a part of the woods. The Sparrow Hawks are evident on any day as they ride the winter wind or balance on the spire of some dead tree. Bluejays are quiet, for once, and wait clumsily for spring. Crows crowd into the woods at evening or feed erratically there throughout the day, but more frequently seek the thicker woods in the valley. They are hunted vigorously by boys of the vicinity and during the previous year 96 were killed in the woods by one hunter. The titmouse is small but conspicuous by its voice. Woodpeckers, including the Downy, Hairy, and Red-bellied, and the Yellow-bellied Sapsucker, are evident in their undulating flight from tree to tree. These birds withstand the winter. There are no sparrows, for there is little cover from the searching hawks or from the wind. Cardinals appear occasionally enroute to more comfortable surroundings.

Spring is a different story. As early as late February and early March migrants begin to arrive. Loud thrasher songs begin in April and Bewick Wrens try out their collection of unfinished calls. May is the magic time. When the leaves come out the flame of Blackburnian Warblers and redstarts flash in the new green. Whole schools of warblers search restlessly, even in the rain. Then, as suddenly, the trees are empty, and occupied with the solemn business of secluding nesting birds.

It is interesting to compare the development of the bird-nesting season (fig. 5, No. 8) with flower bloom (fig. 5, No. 3). Both are influenced to a great extent by the leafing of trees, though in opposite ways, and while the peak of spring bloom is about the last week of April, just before the woods becomes shaded with new leaves, the nesting peak begins in the first week of May. Data on fall migrations were not obtained and consequently the curve in fig. 5, No. 7, is incomplete.

Figure 6 shows the distribution of 51 birds' nests which were discovered within the 41.5 acres of Wildwood. Of these, 5 were second nests of bluejays and 1 of a Bewick Wren. If we consider only first nestings there would be 45, or 1.1 nests per acre. This would mean a resident population of 90 birds or 2.2 mature birds per acre (ignoring the possibilities of polygamy). The total number of birds, assuming production of two young birds per nest (a generous estimate), would

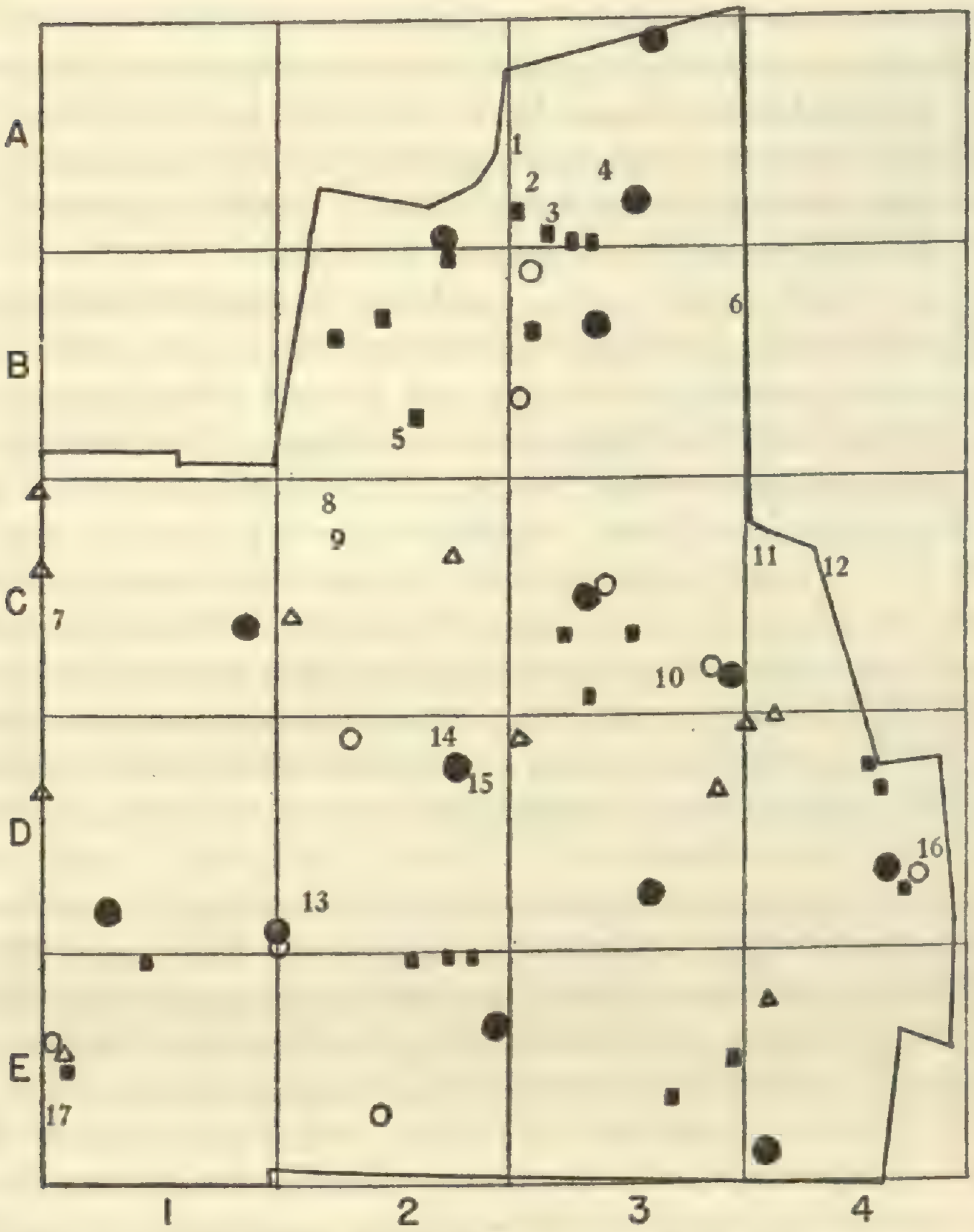

Fig. 6. Distribution of nests in Wildwood. Black dots—Red-headed Woodpecker; white circles—Flicker; black squares—Squirrel; triangle—Bluejay.

Number—as follows:

1. Bewick Wren
2. Bewick Wren
3. Crow
4. Hairy Woodpecker
5. Mourning Dove
6. Yellow-billed Cuckoo
7. Grackle
8. Titmouse
9. Robin
10. Red-bellied Woodpecker
11. Screech Owl
12. Thrasher
13. Crow
14. Wood Duck
15. Sparrowhawk
16. Sparrowhawk
17. Bluebird

have been, about the middle of June, 180 birds, or 4.3 birds per acre. Subsequent to this, second broods were raised in 10 Red-headed Woodpeckers' nests and in 1 Sparrow Hawk nest, and in the second nests of 5 bluejays and 1 Bewick Wren. If an average of two young birds per nest is assumed, 34 birds are added. This is a total of 214 birds.

Early in March the starlings began nesting and continued into August, though to a very much decreased extent. The first nesting was uniform and by far the

most important. It was begun early enough so that little conflict with other birds resulted. The fact that the starlings had chosen their nests made it easier on the Red-headed Woodpeckers to choose theirs when they arrived. There was very little quarreling. When the young starlings hatched there was some friction but nothing to suggest that the starling was causing the Redhead to suffer. The great number of nest holes probably eased some of the tension.

An estimate of the nesting starling population was made in early April. The later nestings were erratic and did not involve more than a few birds. The early nests were thickly concentrated, as many as 5 an acre. Those zones containing the highest percentages of dead Shingle Oaks and Slippery Elms were used. There were about 20 nests during the April nesting. This would mean 40 adults, assuming complete pairing, and 40 young. Added to the previous total of 214 this gives 294 birds in 41.5 acres or 7 birds per acre. The total production of young in the woods would have amounted to 186 from 130 old birds. These figures would not represent the population of the woods at any given time, but serve only to suggest their productivity in terms of bird life. Actually the pressure generated within the woods kept many birds busy along the borders and in adjacent fields. Starlings, once old enough to flock, gathered in the woods about cattle, or as frequently in the vicinity of the cow barns.

In the diagrammatic representation of the birds nests (fig. 6), one fact is most vividly demonstrated—the territorial distribution of Red-headed Woodpecker nests. Flicker nests also show a similar tendency, but being less numerous do not create as striking a pattern. After discovering the first 8 or 9 Redhead nests, I was able to predict where they should be found—simply a matter of waiting at a likely tree in the proper location. If no bird showed itself immediately, it was usually due to late mating; in a few weeks, by returning to the likely place, a nest was almost sure to be discovered. Fourteen nests were found of which 5 were predicted. Uniformity of habitat has much to do with the expression of territoriality. Where ideal conditions extend over sufficient area the manifestations of the behavior pattern have free rein to achieve an equilibrium.

Territories of the Redheads were defended carefully and consistently, but not with any great vengeance. A cautioning call, a flight in the general direction and the intruder left. Birds of other species were not objected to, as Redheads twice nested in the same trees with flickers and one Redhead built three feet from a Sparrow Hawk nest. When the young woodpeckers left the nest tree they gave evidence of a general conception of the adults' territory, but this may have been produced by their desire to remain near the parent bird for food, or by a natural disinclination to wander into unknown parts. During the second nesting of the Redheads defense of their territories became more of a problem, mostly as a result of intruding young of the first brood. These immature trespassers were promptly driven out. Special dispensations seem to have operated during mulberry and blackberry seasons so that traveling woodpeckers could pass through enemy territory unharmed, so long as they stayed on an established flight lane.

A Pileated Woodpecker was seen in late August, but none was seen to nest. There was ample evidence in the form of large squarish holes in many trunks that some time earlier this large woodpecker had been a common resident. The Wood Duck that nested in June was somewhat of a surprise, since it is commonly found nearer the Mississippi. Green Herons seemed strange visitors about the naked ponds, for there was no vegetation to conceal them, but a quick meal of tadpoles or small frogs was too much to resist.

Birds of more open country such as the Dickcissel, Meadowlark, Kingbird, Barn Swallow, and Indigo Bunting were only casual visitants and generally confined their activity to the fence-lines or the free air above the woods. None of these species nested in the woods, for the environment was not at all adaptable. Wildwood is essentially a woodpecker heaven, and of all the woodpeckers, the versatile Redhead seemed most comfortably settled and at home. His methods of feeding and nesting were admirably adapted.

It was no coincidence that the bird population included many species which fed by mounting low limbs, fence-posts, or stumps to watch for passing insects on the ground. Red-headed Woodpeckers, bluejays, bluebirds, Olive-backed and Hermit Thrushes, Sparrow Hawks and thrashers all participated regularly in this drop-to-the-ground method of feeding. Others such as cowbirds, starlings, grackles, and robins promenaded over the greensward itself, the first three species usually in the company of cows which uncovered and disturbed numerous insects and grubs which the patronizing blackbirds bowed to retrieve. Those birds which liked brush and bushes were frequenty visitors but rarely residents. Bewick Wrens took residence in two different fallen trunks and a thrasher nested in a growth of blackberries along the fence just out of the cows' reach. Most of these birds, however, such as the Catbird, Towhee, Swamp Sparrow, White-throated and Winter Wren were only present during migrations, or at times of bathing at the spring.

The analysis of the bird population of Wildwood is a subject that is inclined to lead one into a pleasant afternoon of thought, or an occasional morning of rare peace as the various species reveal their waking hours by their first song. A less aesthetic point of view might be desirable, but this study of Wildwood was never intended to be an altogether coldly analytical calculation of a beautiful place.

Conclusion

Wildwood is an isolated woodland which is slowly becoming more isolated. The slow progress of man across the fertile prairie and the rolling, thinly timbered land of St. Louis County which began in the eighteenth century has not stopped, and will not stop in the twentieth century. The resilient land, once soft with humus and rich with life, now produces sterile streets and careful rows of houses instead of wood or food. People call the soil "real-estate". Wildwood hangs on the verge of destruction. As a sanctuary of impressive beauty the woods can last only a little longer.

Wildwood was once a man's dream and then a man's possession. Major LaMotte, with pride and satisfaction, while on a trip east in 1875, wrote to his wife:

> We have seen so many sights, so much that is novel and interesting, that it appears a 'coons age' since we left Wildwood. But amid all this rambling 'thru pleasures and palaces', thru the charming and beautiful of this world's scenes, we invariably recur to the last word of the song, and apply them, with renewed warmth, to the land we left behind, that dear old Wildwood home.

Wildwood remains as a memorial to a man and a time. These ancient trees are strangely uneasy in 1953. They could crush a cluster of bungalows with the drop of a limb. They grew in the free earth, knowing only the lights of stars at night. They thrived on freedom, and the closing in of twentieth-century men upon them is a saddening, inevitable thing. It is the imminence of their destruction that has prompted me to know their story, to preserve them in words and figures, and in my understanding. They hold within them a part of the secret of life and of environments, part of the mystery of how this earth is organized. Their history is as important as mine.

SUMMARY

A 40-acre woodlot 12 miles northwest of St. Louis was studied for a year from a broad ecological point of view with the object of recording its history, flora, and fauna before it is subdivided. The land was granted to a settler in 1799 by the Spanish governor. Through successive transfers the price rose from $1 an acre in 1804 to $30 in 1851, $300 in 1934, and $1000 in 1946. Exploitation of the land by the owner of a large estate began about 1850. Grazing has been permitted in the woods for nearly 100 years. Changes in the fortunes of the owners are reflected in the composition of the woodland.

Surveys made in 1817-18 described the land as being on the edge of the prairie, with scattered oak and hickory. Testimony of the surveyors concerned and contemporary travelers indicate the importance of fire in maintaining the grassland, and call attention to the influx of trees with settlement, these decreasing in size away from the towns. A soil survey of the area indicates the prairie of 1818 extended eastward over forest soil.

The entire tree population was plotted and found to average 19 trees per acre, with nearly one fifth of these recently dead. Over 54 per cent of the woods is made up of Shingle Oak, Black Oak and Pignut Hickory.

Ages of 222 trees in Wildwood were taken and the year of origin thus determined. These data suggest an increase in tree sprouting in the late eighteenth century, with an especially strong influx of Shingle Oaks between 1800 and 1830. Ages of witness trees from three early surveys substantiated this. Exploratory methods of using data from old surveys to determine density of woodlands are suggested. Rates of growth in the woods were very high, ranging from 1.7 to 7 years per inch. Sassafras, Shingle, Black, and Blackjack Oaks and one hickory over 200 years old were found.

The flora reflects the dynamic conditions that prevail in the woods, with cows,

fire, and fallen trees playing the major roles. Neither prairie nor woodland species are prominent. Curves of flowering peaks and flower initiation are presented and compared to those of other habitats. A hasty survey of plant cover under trees indicates less than 35 per cent edible forage in shaded areas. Grazing is at the rate of 2 head per acre from April to December, resulting in considerable erosion.

Bird and animal populations are described, and a survey of bird nests showed 71, with 11 second broods. The territorial distribution of Red-headed Woodpecker nests and flicker nests is described.

Epilogue

A few days after the manuscript for this paper had been sent in to the editor, circumstances permitted an early morning visit to Wildwood. My breath stopped when I came to the top of the hill where I had many times entered the woods. Instead of coming into the long shadows of its tall trees there was a gaping hole in the landscape. While the old mansion still remained secluded behind its curtain of Black Locust, the woods was gone—not a tree, not a plant, not a fence nor a cow. The long green sweep of pasture was a hill of yellow dirt yielding on every hand to bulldozers and scoops. The first row of skimpy houses was already up. On the wall of a shed was a plat of the development. I could not believe the ironic name it displayed. Forestwood! Not one of its future residents will be able to fathom why. The main street will be Meadowcrest—though asphalt and cement will cover the meadow.

Thus it is that we destroy the things we love the most! But I am thankful for one thing. The old farmer that had lived to 86 and for 50 years had milked Wildwood's cows by hand died only a few days before the first trees fell, and he will remember the woods as I have tried to describe it.

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APPENDIX I

PARTIAL LIST OF PLANT SPECIES FOUND IN WILDWOOD

(Arranged in natural order from Fernald, 1950)

Bromus secalinus L., Cheat
Poa annua L., Annual Bluegrass
Poa pratensis L., Kentucky Bluegrass
Dactylis glomerata L., Orchard Grass
Hordeum pusillum Nutt., Little Barley
Agrostis perennans (Walt.) Tuckerm., Upland Bent
Muhlenbergia Schreberi J. F. Gmel., Nimble Will
Eleusine indica (L.) Gaertn., Wiregrass
Digitaria sanguinalis (L.) Scop., Crab-Grass
Setaria glauca (L.) Beauv., Foxtail
Arisaema Dracontium (L.) Schott, Green Dragon
Commelina communis L., Creeping Dayflower
Juncus tenuis Willd.
Polygonatum canaliculatum (Muhl.) Pursh, Solomon's-Seal
Smilax herbacea L., Carrion-flower
Hypoxis hirsuta (L.) Coville, Stargrass
Sisyrinchium campestre Bicknell, Prairie Blue-eyed Grass
Salix nigra Marsh., Black Willow
Populus deltoides Marsh., Cottonwood
Juglans nigra L., Black Walnut
Carya ovata (Mill.) K. Koch, Shagbark Hickory
Carya tomentosa Nutt., Mockernut
Carya ovalis (Wang.) Sarg., Pignut Hickory
Quercus alba L., White Oak
Quercus stellata Wang., Post Oak
Quercus rubra L. var. *borealis* (Michx. f.) Farw., Northern Red Oak
Quercus velutina Lam., Black Oak
Quercus marilandica Muench., Black Jack
Quercus imbricaria Michx., Shingle Oak
Ulmus americana L., White Elm
Ulmus rubra Muhl., Slippery Elm
Celtis occidentalis L., Hackberry
Morus rubra L., Red Mulberry
Morus alba L., White Mulberry
Cannabis sativa L., Hemp
Urtica procera Muhl., Slender Nettle
Laportea canadensis (L.) Wedd., Wood-Nettle
Rumex crispus L., Yellow Dock
Rumex Acetosella L., Sheep Sorrel
Polygonum pensylvanicum L., Pinkweed
Polygonum Hydropiper L., Smartweed
Polygonum Persicaria L., Lady's Thumb
Chenopodium album (L.)., Lamb's Quarters
Chenopodium ambrosioides L., Mexican Tea
Phytolacca americana L., Pokeweed
Claytonia virginica L., Spring-beauty
Mollugo verticillata L., Carpetweed
Stellaria media (L.) Cyrillo, Common Chickweed
Stellaria pubera var. *silvatica* (Beguinot) Weath., Great Chickweed
Silene stellata (L.) Ait. f., Starry Campion
Ranunculus micranthus Nutt., Buttercup
Delphinium tricorne Michx., Dwarf Larkspur
Podophyllum peltatum L., May-apple
Sassafras albidum Nutt. var. *molle* (Raf.) Fern., Red Sassafras
Cleome spinosa Jacq., Spider-flower
Draba brachycarpa Nutt., Short-fruited Whitlow Grass
Thlaspi arvense L., Field Penny-Cress
Lepidium virginicum L., Peppergrass
Capsella Bursa-pastoris (L.) Medic., Shepherd's Purse
Sisymbrium officinale (L.) Scop., Hedge-Mustard
Platanus occidentalis L., Sycamore
Fragaria virginiana Duch. var. *illinoensis* (Prince) Gray, Wild Strawberry
Potentilla simplex Michx., Cinquefoil
Prunus serotina Ehrh., Black Cherry
Gleditsia triacanthos L., Honey-Locust
Trifolium repens L., White Clover
Robinia Pseudo-Acacia L., Black Locust
Oxalis violacea L., Violet Wood-Sorrel
Oxalis europaea Jord. f. *pilosella* Wieg., Yellow Wood-Sorrel
Geranium carolinianum L., Cranesbill
Ailanthus altissima (Mill.) Swingle, Tree of Heaven
Acalypha gracilens Gray, var. *monococca* Englm., Three-seeded Mercury
Acalypha ostryaefolia Riddell
Euphorbia maculata L., Eyebane
Callitriche deflexa A. Br., var. *Austini* (Englm.) Hegelm.
Rhus radicans L., Poison Ivy
Acer saccharum Marsh., Sugar Maple
Acer saccharinum L., Silver Maple
Acer Negundo L., Box-Elder
Parthenocissus quinquefolia (L.) Planch., Virginia Creeper

Vitis vulpina L., Frost or Chicken-Grape
Hypericum punctatum Lam., St. John's-Wort
Viola papilionacea Pursh, Meadow or Common Violet
Viola sororia Willd., Woolly Blue Violet
Viola pensylvanica Michx., Smooth Yellow Violet
Viola Kitaibeliana R. & S. var. *Rafinesquii* (Greene) Fern., Field Pansy
Sanicula canadensis L., Black Snakeroot
Osmorhiza longistylis (Torr.) DC., Smooth Sweet Cicely
Cornus racemosa Lam., Gray Dogwood
Diospyros virginiana L., Persimmon
Asclepias syriaca L. var. *kansana* (Vail) Palmer & Steyermark., Common Milkweed
Gonolobus Baldwinianus Sweet, Climbing Milkweed
Elissia Nyctelea L., Aunt Lucy
Verbena urticifolia L., White Vervain
Verbena stricta Vent., Hoary Vervain
Lippia lanceolata Michx. var. *recognita* Fern. & Grisc., Fog-fruit
Teucrium canadense L. var *virginicum* (L.) Eat., Wood-Sage
Nepeta Cataria L., Catnip
Glechoma hederacea L. var. *micrantha* Moricand, Ground-Ivy
Prunella vulgaris L., Heal-all
Lamium amplexicaule L., Henbit
Monarda fistulosa L., Wild Bergamot
Monarda citriodora Cerv., Lemon-Mint
Hedeoma pulegioides (L.) Pers., American Pennyroyal
Melissa officinalis L., Common Balm
Pycnanthemum virginianum (L.) Durand & Jackson, Mountain Mint
Mentha spicata L., Spearmint
Solanum nigrum L., Black Nightshade
Solanum carolinense L., Horse-Nettle
Physalis pumila Nutt., Ground-cherry
Datura Stramonium L. var. *Tatula* (L.) Torr., Purple Thorn-Apple
Verbascum Thapsus L., Common Mullein
Verbascum Blattaria L., Moth Mullein
Verbascum Blattaria f. *albiflorum* (Don) House
Scrophularia marilandica L., Figwort
Penstemon Digitalis Nutt., Beard-Tongue
Mimulus ringens L., Monkey Flower
Plantago major L., Plantain
Plantago Rugelii Dcne., Plantain
Plantago lanceolata L., Ribgrass
Galium Aparine L., Goosegrass
Houstonia minima Beck, Bluets
Sambucus canadensis L., Common Elderberry
Specularia perfoliata (L.) A. DC., Venus' Looking-Glass
Campanula americana L., Tall Bellflower
Lobelia siphilitica L., Blue Lobelia
Lobelia inflata L., Indian-tobacco
Vernonia altissima Nutt., Ironweed
Vernonia Baldwini Torr., Ironweed
Eupatorium serotinum Michx., Thoroughwort
Eupatorium rugosum Houtt., White Snakeroot
Eupatorium coelestinum L., Mistflower
Erigeron philadelphicus L., Fleabane
Erigeron annuus (L.) Pers., Daisy Fleabane
Erigeron strigosus Muhl., Daisy Fleabane
Erigeron canadensis L., Horse-weed
Gnaphalium purpureum L., Purple Cudweed
Ambrosia trifida L., Great Ragweed
Ambrosia artemisiifolia L. var. *elatior* (L.) Desc., Common Ragweed
Rudbeckia hirta L., Black-eyed Susan
Achillea Millefolium L., Common Yarrow
Chrysanthemum Leucanthemum L. var. *pinnatifidum* Lecoq & Lamotte, Ox-eye Daisy
Cirsium vulgare (Savi) Tenore, Common or Bull Thistle
Cichorium Intybus L., Chicory
Taraxacum officinale Weber var. *palustre* (Sm.) Blytt, Common dandelion
Lactuca scariola L., Prickly Lettuce

Appendix II

LIST OF BIRD SPECIES FOUND IN WILDWOOD

(Nomenclature from Bennitt, 1932)

Great Blue Heron, *Ardea herodias herodias*
Eastern Green Heron, *Butorides virescens virescens*
Wood Duck, *Aix sponsa*
Sharp-shinned Hawk, *Accipiter velox velox*
Eastern Sparrow Hawk, *Falco sparverius sparverius*
Eastern Bob-white, *Colinus virginianus virginianus*
Killdeer, *Oxyechus vociferus vociferus*
Eastern Solitary Sandpiper, *Tringa solitaria solitaria*
Rock Dove, *Columbia livia livia*
Eastern Mourning Dove, *Zenaidura macroura carolinensis*
Yellow-billed Cuckoo, *Coccyzus americanus americanus*
Eastern Screech Owl, *Otus asio naevius*
Eastern Nighthawk, *Chordeiles minor minor*
Chimney-swift, *Chaetura pelagica*
Ruby-throated Hummingbird, *Archilochus colubris*
Eastern Belted Kingfisher, *Megaceryle alcyon alcyon*
Northern Flicker, *Colaptes auratus luteus*
Northern Pileated Woodpecker, *Ceophloeus pileatus abieticola*
Red-bellied Woodpecker, *Centurus carolinus*
Red-headed Woodpecker, *Melanerpes erythrocephalus*
Yellow-bellied Sapsucker, *Sphyrapicus varius varius*
Eastern Hairy Woodpecker, *Dryobates villosus villosus*
Northern Downy Woodpecker, *Dryobates pubescens medianus*
Eastern Kingbird, *Tyrannus tyrannus*
Northern Crested Flycatcher, *Myiarchus crinitus boreus*
Eastern Phoebe, *Sayornis phoebe*
Least Flycatcher, *Empidonax minimus*
Eastern Wood Pewee, *Myiochanes virens*
Barn Swallow, *Hirundo erythrogaster*
Purple Martin, *Progne subis subis*
Northern Bluejay, *Cyanocitta cristata cristata*
Eastern Crow, *Corvus brachyrhynchos brachyrhynchos*
Tufted Titmouse, *Baeolophus bicolor*
Red-breasted Nuthatch, *Sitta canadensis*
Brown Creeper, *Certhia familiaris americana*
Western House Wren, *Troglodytes aedon parkmani*
Eastern Winter Wren, *Nannus hiemalis hiemalis*
Bewick's Wren, *Thryomanes bewicki bewicki*
Eastern Mockingbird, *Mimus polyglottos polyglottos*
Catbird, *Dumetella carolinensis*
Brown Thrasher, *Toxostoma rufum*
Eastern Robin, *Turdus migratorius migratorius*
Wood Thrush, *Hylocichla mustelina*
Eastern Hermit Thrush, *Hylocichla guttata faxoni*
Eastern Olive-backed Thrush, *Hylocichla ustulata swainsoni*
Eastern Blue Bird, *Sialia sialis sialis*
Blue-grey Gnatcatcher, *Polioptila caerulea caerulea*
Eastern Golden-crowned Kinglet, *Regulus satrapa satrapa*
Eastern Ruby-crowned Kinglet, *Corthylio calendula calendula*
Cedar Waxwing, *Bombycilla cedrorum*
Starling, *Sturnus vulgaris vulgaris*
Yellow-throated Vireo, *Vireo flarifrons*
Blue-headed Vireo, *Vireo solitarius solitarius*
Red-eyed Vireo, *Vireo olivaceus*
Eastern Warbling Vireo, *Vireo gilvus gilvus*
Black-and-white Warbler, *Mniotilta varia*
Magnolia Warbler, *Dendroica magnolia*
Myrtle Warbler, *Dendroica coronata*
Black-throated Green Warbler, *Dendroica virens virens*
Blackburnian Warbler, *Dendroica fusca*
Chestnut-sided Warbler, *Dendroica pensylvanica*
Western Palm Warbler, *Dendroica palmarum palmarum*
Northern Yellow-throat, *Geothlypis trichas brachidactyla*
American Redstart, *Setophaga ruticilla*
English Sparrow, *Passer domesticus domesticus*
Eastern Meadowlark, *Sturnella magna magna*
Eastern Red-wing, *Agelaius phoeniceus phoeniceus*
Orchard Oriole, *Icterus spurius*
Baltimore Oriole, *Icterus galbula*

Bronzed Grackle, *Quiscalus quiscula aeneus*
Eastern Cowbird, *Molothrus ater ater*
Scarlet Tanager, *Piranga erythromelas*
Summer Tanager, *Piranga rubra rubra*
Eastern Cardinal, *Richmondena cardinalis cardinalis*
Rose-breasted Grosbeak, *Hedymeles ludovicianus*
Indigo Bunting, *Passerina cyanea*
Dickcissel, *Spiza americana*
Eastern Purple Finch, *Carpodacus purpureus purpureus*
Eastern Goldfinch, *Spinus tristis tristis*
Red-eyed Towhee, *Pipilo erythrophthalmus erythrophthalmus*
Slate-colored Junco, *Junco hyemalis hyemalis*
Eastern Chipping Sparrow, *Spizella passerina passerina*
White-throated Sparrow, *Zonotrichia albicollis*
Swamp Sparrow, *Melospiza georgiana*

EXPLANATION OF PLATE

PLATE 27

Two views of Wildwood in 1952.

ETTER—WILDWOOD

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Some X-Ray Effects in *Petunia*.....Henry A. McQuade 259–270
Some Lichens of Tropical Africa.....Carroll W. Dodge 271–401
General Index to Volume XL..... 403–412

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Annals
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SOME X-RAY EFFECTS IN PETUNIA[1]

HENRY A. McQUADE

Of 945 *Petunia* plants grown from seed arising from x-irradiated sperms and untreated eggs or from untreated sperms and x-irradiated eggs, 907 reached maturity. Forty-three diploid (n = 7) controls were grown simultaneously. The following classes were represented:

1. *Seed from normal eggs fertilized by sperms from pollen grains receiving 13,200 r to 18,000 r at increments of 600 r (nine groups).*—There were three additional groups of seed arising from pollen treated at 20,000, 22,200, and 25,800 r. Plants from these seeds are referred to hereafter by the dosage number as well as plant number.

2. *Seed derived from treated eggs fertilized by untreated sperms.*—In this class ovaries were treated with 2,400 and 3,000 r. Plants arising from these seeds are referred to hereafter as ♀ 2,400 and ♀ 3,000 r as well as by plant number.

3. *Seed from untreated eggs fertilized by sperms from pollen grains treated prior to anthesis when the anthers were turgid.*—Plants from such seeds are referred to as Anther 5,400 or Anther 6,600 as well as by plant number.

Of the 945 plants, 206 showed effects of x-ray treatment; 38 of these died during the following growing season presumably because of such treatment. There was no damage apparent in 739 plants, but an effort was made to determine whether or not these phenotypically normal individuals were affected.

Methods.—Technical factors for irradiation were: target distance 15 cm., filter ½ mm. of aluminum, 120 KV, 10 milliamps, H.V.L. = 1.6 mm. of aluminum.

Mature pollen (seed Class 1) was treated by putting the pollen in No. 2 gelatin capsules, fastening the capsules on a stage of Scotch tape and centering them carefully under the target. In treating ovaries (Class 2) the flowers were held in place with strips of Scotch tape on the ring stage. Lead shields protected

[1]Thanks are due Dr. George T. Moore, Director, for use of the Missouri Botanical Garden facilities, and to Dr. Hugh M. Wilson, Director, Mallinckrodt Institute of Radiology, Washington University, where the radiations were carried on.

all flower parts except the ovary. In order to treat pollen prior to anthesis (Class 3) the anthers were placed in a capsule, irradiated, and then allowed to ripen and shatter within the capsule. A more detailed account of the method is to be found in a previous report (McQuade, 1952).

Cross-sections were from paraffin-embedded leaves stained with safranin and fast green; meiotic preparations were aceto-carmine smears. In making pollen counts, those grains which did not stain were scored as non-viable.

PLANTS WITH VISIBLE EFFECTS OF X-RAY TREATMENT

Phenotypes.—Among the abnormal phenotypes certain characters appeared rather frequently:

Leaf.—
1. Surface wrinkled
2. Surface with light spots (pl. 28, fig. 1)
3. Color pale to dark green, the paleness often associated with thinness in cross-section
4. Margin lobed (pl. 28, fig. 2)
5. Outline elliptical to suborbicular (pls. 28 and 29)
6. Margin involute (pl. 28, fig. 3); margin revolute (pl. 30, fig. 5)
7. Variable petiole length, the sessile condition being often associated with the spatulate condition

Stem.—
1. Stiff, strongly upright
2. Thin, soft, weak
3. Fusion between a shoot and pedicel
4. Fasciation (pl. 29, fig. 5)

Flower.—
1. Corolla with numerous white spots (pl. 29, fig. 6)
2. Corolla with spots of various colors including white and pink through purple (pl. 28, fig. 1)
3. Distortion of corolla, corolla-tube, calyx, stamens, pistil (pl. 29, fig. 4)
4. Warty protuberances over corolla
5. Failure to flower

Habit.—
1. Miniature
2. Abundant weak leaders (pl. 29, fig. 3)
3. Tall strong habit associated with strong stem
4. Globose, stunted (pl. 29, fig. 2)
5. Recumbent
6. Rosette

Among the teratological conditions observed were two extreme forms. Plate 29, fig. 1, shows flowers in which calyx members have been superseded by petaloid structures one of which is subtending an anther. In another case, parts of the stigmatic rim developed petaloid or sepaloid structures.

The characters listed were combined in a number of ways. For example, plant 52, 18,000 r, had thin, spotted leaves, weak stems, spotted corollas. Plant 25, 15,600 r, had thick, lobed leaves with light spots and spotted corollas.

Leaf Abnormalities.—Since most of the plants with visible x-ray effects showed leaf abnormalities, attention was given to the morphology in these disorders.

1. Plants 23, 20,000 r, 29, 18,000 r, and others (pl. 30, figs. 1, 2, 3) were characterized by light spots on their leaves. These light areas were found to be thin places and were seen first in material sectioned free-hand. When this was studied in microtomed tissue later, the dark areas were found to contain palisade and spongy parenchymas, and the light or thin spots to consist largely of undifferentiated cells.

2. Plant 26, 25,800 r (pl. 30, figs. 5, 7) had leaves so completely revolute as to be circular in cross-section. The curvature was brought about by a strongly developed upper epidermis opposed by a weak lower epidermis. Mesophyll cells were irregular but tended to be round; the columnar definition of a palisade parenchyma was lacking.

3. Plant 40, 20,000 r (pl. 30, fig. 6) possessed a homogeneous mesophyll the cells of which appeared generally spherical if somewhat irregular in outline. These cells were rather densely packed. Only occasionally was there found a columnar cell reminiscent of a palisade parenchyma and then its long axis was apt to be parallel, rather than perpendicular, to the epidermis.

4. Plant 78, 20,000 r (pl. 30, fig. 4) had a palisade parenchyma which could be identified as such but it represented a squat rather than normal cell type.

Cytological Data.—Cytological data were gathered on thirteen plants with visible radiation effects. These plants represented dosage groups 16,200 r, 17,400 r, 20,000 r, 25,800 r, applied to mature pollen, ovaries treated at 2400 r, and unripe anthers treated with 5,400 r. Where controls showed a normal meiosis these obviously affected individuals were characterized by some of the following disorders:

1. The presence of fragments.
2. A chromosome or chromosomes not taking the customary position on the equatorial plate at metaphase I or II.
3. The presence of an extra chromosome at a pole or the absence of a chromosome at a pole following anaphase I.
4. Pollen tetrad abnormalities in the form of micro-grains, in addition to the four nuclei characteristic of this stage, or fewer than four nuclei at conclusion of telophase II. Occasionally large nuclei were found after telophase II.
5. Disorganization of the metaphase I plate to such an extent that a plate might consist of several clumps of bivalent chromosomes. Often these clumps of bivalents were oriented in different dirctions.

The following cytological observations on five plants give a fair picture of the meiotic disorders generally encountered.

1. Plant 23, 20,000 r, was the first plant in which the leaf spots were investigated (pl. 30, fig. 1). Its flowers were miniature and produced little pollen; when enough pollen was finally gathered for a count, it proved to be 92.67 per cent non-viable.

Apparently normal telophase II cells	18
4 nuclei + 1 micro-nucleus	14
2 nuclei only	4
2 nuclei + 1 micro-nucleus	3
1 nucleus only	2
3 nuclei	2
3 nuclei + 1 micro-nucleus	6
3 nuclei + 2 micro-nuclei	1
	50

Additional pollen tetrad material indicated extensive disorder in which one or more nuclei were malformed and some nuclei appeared diffuse.

2. Plant 37, 20,000 r, possessed leaves with light spots and corollas that were spotted. Its pollen was 48.04 per cent non-staining; when selfed it did not set seed.

Diakinesis cells with 7 bivalent chromosomes	8
Diakinesis cells with 7 bivalents + 1 large fragment	10
	18
Apparently normal anaphase I cells	83
Cells with bridges or bridges + fragments	25
Cells with lagging chromosome or fragment	12
	120

Among these anaphase I cells was one in which 7 chromosomes could be counted at one pole, 6 at the other, with a laggard between.

3. Plant 55, 25,800 r, had leaves which were spotted and mildly lobed. Its corollas were spotted, and one pedicel was partially fused to the shoot from which it arose. Its pollen grains were 98.66 per cent non-staining.

Apparently normal metaphase I cells	9
Cells with 1 bivalent off plate	11
Cells with 2 bivalents off plate	3
Cells with 3 bivalents off plate	1
	24

Other cells were found in which bivalents were arranged in several clumps, some improperly oriented.

Apparently normal anaphase I cells	1
Cells with 1 bivalent between poles	1
	2
Apparently normal telophase II cells	6
Cells with no chromatin at one pole	3
	9

4. Plant 76, ♀ 2,400 r, exhibited spotted leaves and corollas.

Apparently normal metaphase II cells	125
a. 7 chromosomes at one plate, other plate undetermined	13
b. 7 chromosomes at both plates	2
c. Chromosome numbers undetermined but no laggards or fragments present	110
Abnormal metaphase II cells	77
a. 1 chromosome or large fragment between plates or at one side	52
b. 7 chromosomes on one plate, other uncounted; laggard between plates	1
c. 7 chromosomes on one plate, 6 on other; laggard between plates	3
d. 7 chromosomes on one plate, 6 on other; no laggard	1
e. 8 chromosomes on one plate, 6 on other	2
f. 8 chromosomes on one plate, other uncounted	3
g. One bridge or remains of bridge	15
	202
Apparently normal tetrads	91
Tetrad + 1 micro-nucleus	25
Tetrad + 2 micro-nuclei	2
	118

Distribution of chromosomes is therefore seen to be irregular at telophase II. In one cell, for example, there were two groups of 7 chromosomes, one group of 6, one small undetermined group, and 2 chromosomes at separate points not belonging to any particular groups.

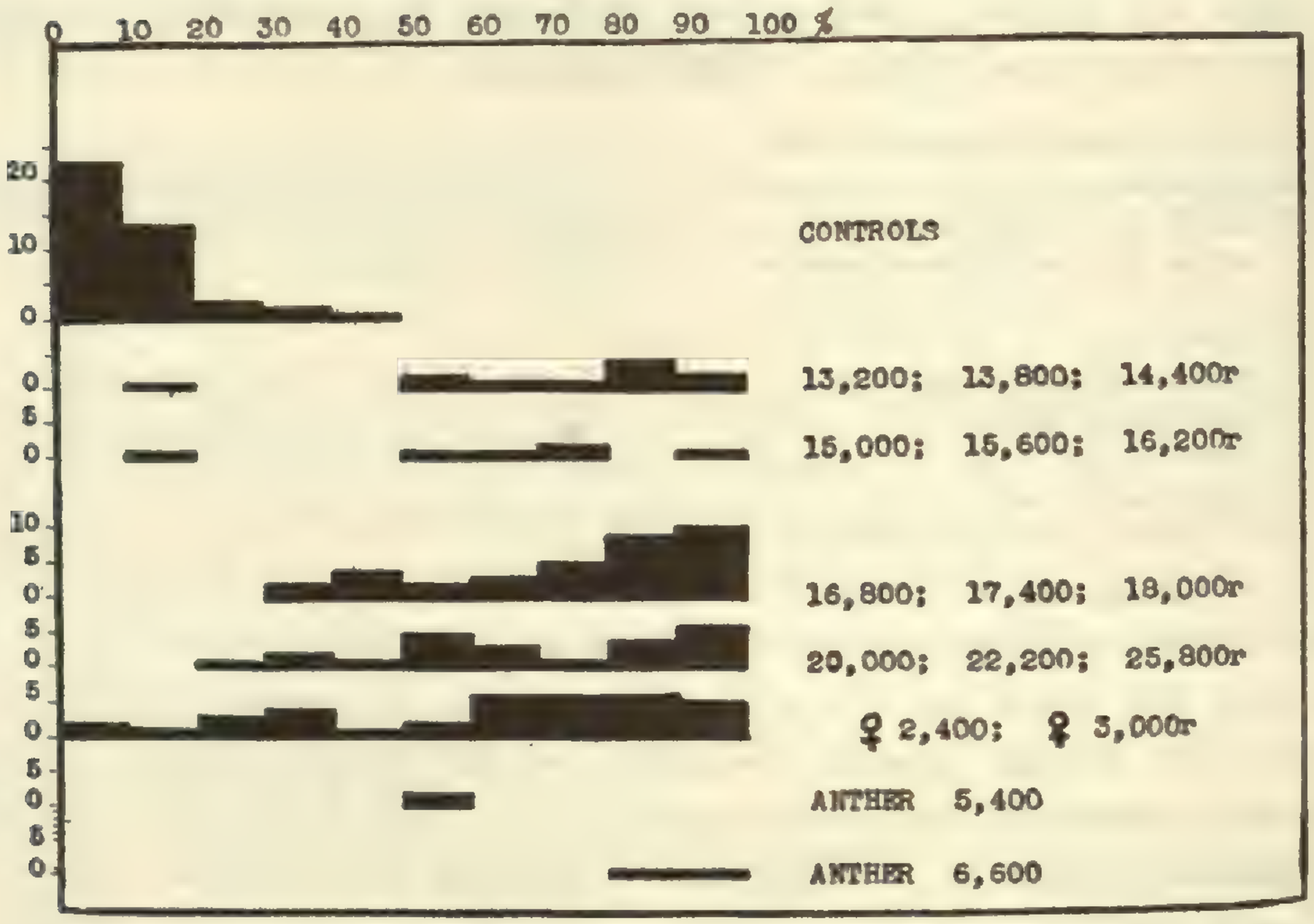
5. Plant 69, Anther 5,400 r, had 56.95 per cent non-staining pollen. Its flowers were white to pale pink, its leaves spatulate.

Apparently normal telophase II cells	64
Abnormal cells	38
4 nuclei + 1 micro-nucleus	1
3 nuclei + 1 malformed nucleus	19
2 nuclei + 2 malformed nuclei	8
3 nuclei only	1
3 malformed nuclei only	2
4 malformed nuclei	5
1 large nucleus only	1
2 large nuclei only	1
	102

Pollen Counts.—Pollen counts were made on 130 plants showing x-ray effects. Counts were not made on 20, and 18 produced no pollen because they did not flower, the meiotic system collapsed, or for other reasons. Individuals were classified according to percentage of visibly non-viable (i.e. non-staining) pollen produced (Table I). While the 43 controls showed some variation with regard to non-staining pollen, a glance at text-fig. 1 indicates that those plants showing x-ray effects tended to have high percentages of non-viable pollen. Since dosage delivered may have varied ± 10 per cent, the class frequencies of non-staining pollen grains were lumped as indicated to produce text-figs. 1 and 2.

TABLE I

Treatment	Number of plants	Plants producing no pollen	Plants in which no counts were made	Classes: per cent non-staining pollen									
				0 –10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
	Controls												
None	43			23	14	3	2	1					
	Plants with visible X-ray effects												
13,200 r	9	1	1		1				1	1		3	1
13,800 r	2										1		1
14,400 r	2								1			1	
15,000 r	3	1	1						1				1
15,600 r	5	1			1				1	1	1		
16,200 r	4	2									1		1
16,800 r	7							1				2	4
17,400 r	16	1	2					2	1	1	2	4	3
18,000 r	21	2	4				2	1	1	2	3	3	3
20,000 r	34	5	6			1	2	1	5	3	1	4	6
22,200 r	1										1		
25,800 r	18	2	3							1	5	2	5
♀ 2,400 r	36	1	3	2	1	3	4	1	2	6	4	5	4
♀ 3,000 r	4										2	1	1
Anther 5,400 r	2								2				
Anther 6,600 r	4	2										1	1
	168	18	20										



Text-fig. 1. Controls and plants showing x-ray effects. Figures at left represent numbers of individuals per class; those at top, per cent of non-staining pollen.

PLANTS SHOWING NO VISIBLE X-RAY EFFECTS

Cytological Data.—Cytological observations were gathered on five plants. Unfortunately no data were gathered in plants where the percentages of non-staining pollen grains were in the high ranges.

1. Plant No. 2, 16,200 r, produced pollen grains of which 47.70 per cent did not stain. Of 27 anaphase I cells studied, none showed disorders. In seven of these cells the distribution of chromosomes was determined to be 7 per pole.

2. Plant No. 3, 16,200 r, had 6.01 per cent non-staining pollen. No disorders were observed in the 49 anaphase I cells studied, and the distribution of chromosomes was determined to be regularly 7 per pole.

3. Plant No. 5, 20,000 r, produced pollen of which 48.0 per cent of the grains were non-staining. Examination of anaphase II cells indicated no disorders, with distribution of chromosomes being 7 per pole.

4. For plant No. 12, 20,000 r, no pollen count was made. Examination of 20 anaphase I cells indicated no abnormalities. In 20 of 23 metaphase II cells, 7 chromosomes ready for division were counted on one plate, while on the other plate the chromosomes could not be counted. In the remaining three cells 7 chromosomes ready for division were counted on both plates. No micro-grains were evident in pollen tetrads.

Pollen Counts.—Table II summarizes the pollen counts for phenotypically normal individuals. Text-fig. 2 indicates that these often had high percentages of non-staining pollen as compared to controls.

TABLE II
PHENOTYPICALLY NORMAL INDIVIDUALS

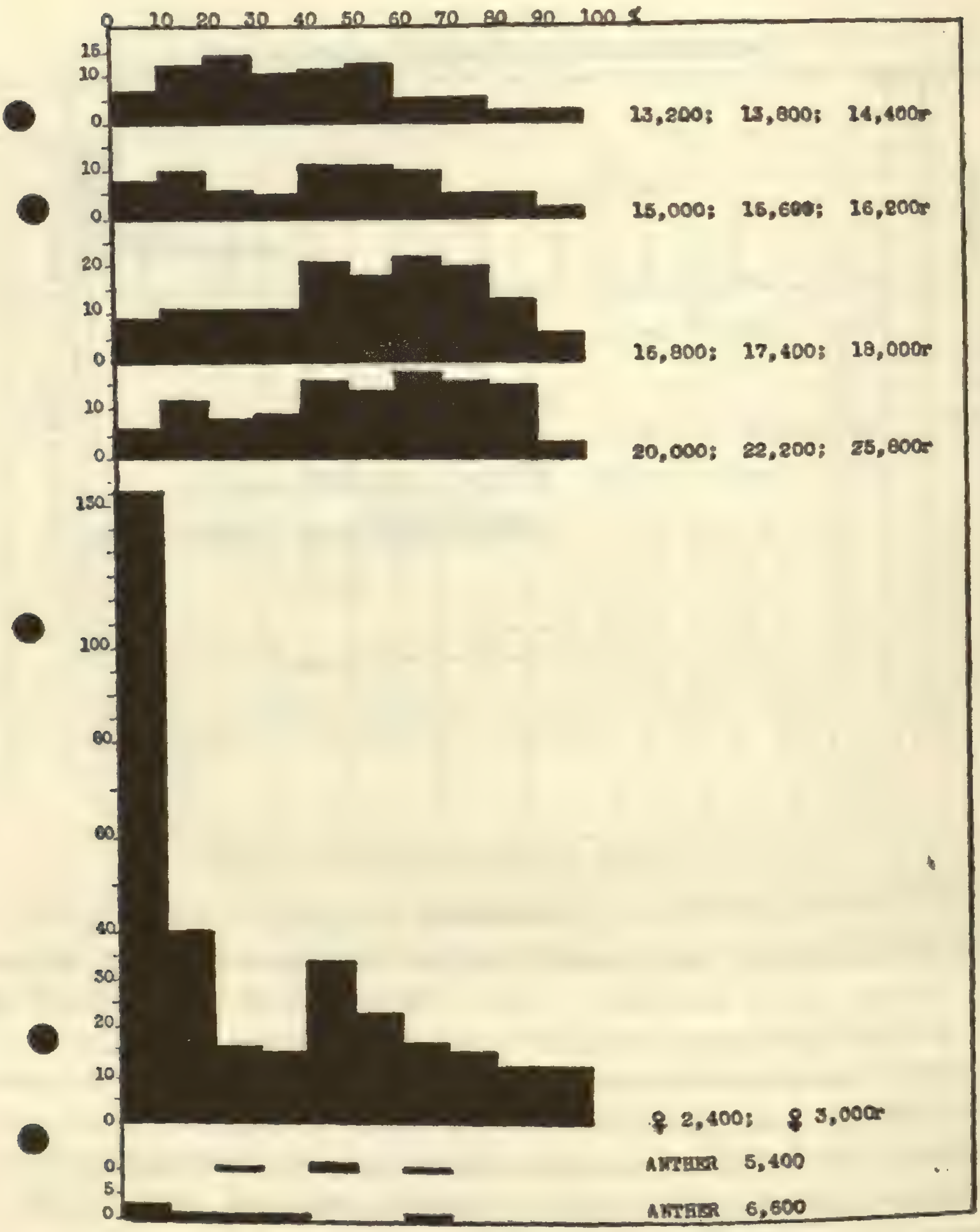
Treatment	No.	Classes: per cent non-staining pollen									
		0 –10	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
13,200 r	32	5	4	6	3	6	6	2			
13,800 r	24	1	3	5	4	1	5	2	2	1	
14,400 r	24	1	5	3	3	4	1	1	3	1	2
15,000 r	27	4	3	1	1	2	4	8	2	2	
15,600 r	30	2	6	5	3	3	6	1	2	1	1
16,200 r	15	2	1		1	6	1	1	1	1	1
16,800 r	15	1	3	2	1		1	3	1	3	
17,400 r	64	4	3	4	7	11	9	10	9	4	3
18,000 r	63	4	5	5	3	10	8	9	10	6	3
20,000 r	88	5	7	6	7	14	11	14	13	11	
22,200 r	10	1	5	1	1			1	1		
25,800 r	19			1	1	2	3	3	2	4	3
♀ 2,400 r	313	133	38	16	15	34	23	17	13	12	12
♀ 3,000 r	4		2						2		
Anther 5,400 r	4			1		2		1			
Anther 6,600 r	7	3	1	1	1			1			
	739										

DISCUSSION

The cytological data were recorded here for the purpose of giving background to the radiation effects mentioned. There is little need to discuss the effects of x-rays on meiotic chromosomes; this has been done at length by Lea (1947), and Rick (1943) who studied *Petunia*. In view of the extensive damage to chromatin in plants showing x-ray effects it is hardly plausible to assign such a character as light spots of the leaf to a particular radiation-induced chromosomal aberration. The widespread x-ray-induced leaf abnormalities may well attest to the large number of loci concerned in leaf development.

It is suggested that in the leaf abnormalities considered here cells often appear undifferentiated rather than differentiated abnormally. In plant No. 40 (pl. 30, fig. 6), the mesophyll cells resemble the undifferentiated cells of tobacco (Avery, 1933) and apple (MacDaniels and Cowart, 1944) near the marginal meristem of the young leaf. In plant No. 78 (pl. 30, fig. 4), the mesophyll reflects somewhat the columnar condition of mesophyll in the young apple leaf during rapid cell division (MacDaniels and Cowart, 1944). In plant No. 26 (pl. 30, figs. 5 and 7), the mesophyll is irregular with some of the upper cells becoming columnar but most of them remaining undifferentiated.

The situation in which a clearly defined epidermis covers an undifferentiated mesophyll (plant 26) is clarified by Avery (1933) who points out that, in tobacco, epidermal cells acquire their characteristic appearance very early but that



Text-fig. 2. Phenotypically normal plants. Figures at left represent numbers of individuals; those at top, per cent of non-staining pollen.

palisade cells do not undergo similar development until the leaf is 4–5 mm. long. Here it seems there has been time enough for some epidermal development before mesophyll development has been halted.

No phenotypic differences were observed between plants grown from seed arising from treated sperms and untreated eggs and plants from seed from untreated sperm and treated eggs.

In general, it appeared that visible radiation effects were associated with a high degree of pollen non-viability although there were some affected plants that had a smaller percentage of non-staining pollen than some with no visible effects. That pollen non-viability could occur independently of visible radiation effects is apparent from text-fig. 2.

It is not suggested that the histograms present a full picture of x-ray effects, since they do not account for the seeds that failed to germinate or individuals that died in the seedling stage. The estimation of pollen non-viability is probably conservative in that pollen grains which stained would not necessarily germinate, or if they germinated might not function properly because of damage of a sort not immediately detectable. For example, plant 37, 20,000 r, with pollen grains of which 48.04 per cent were non-staining did not set seed when selfed; plant 36, 20,000 r, with pollen 64.06 per cent non-staining, set two fruits.

SUMMARY

1. Nine hundred and seven of 945 *Petunia* plants were grown to maturity from seed arising from x-irradiated sperms and untreated eggs or untreated sperms and x-irradiated eggs. Of these, 206 plants showed x-ray effects; 38 died. No effects were apparent in 739 plants.

2. Cytological observations and observations on pollen viability indicated that phenotypic effects of x-ray treatment were usually accompanied by high percentages of pollen non-viability. It was also demonstrated that x-ray treatment often resulted in high percentages of pollen non-viability in plants whose phenotypes were normal.

3. No phenotypic differences were observed in plants in which x-ray effects were brought about through treatment of pollen as opposed to ovaries.

4. The leaf morphology resulting from x-ray treatments described above were considered.

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EXPLANATION OF PLATE 28

1. 20,000 r (Plant 23. See also pl. 30, fig. 1). Light and dark areas on leaf. × about ¼.
2. 15,600 r (Plant 25). Leaf margins lobed. × about ¼.
3. 20,000 r. Leaf margins involute. × about ¼.
4. 18,000 r. Elliptical leaf. × about ½.
5. 20,000 r. Spatulate leaf. × about ½.
6. Control. × about ¼.

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McQUADE—X-RAY EFFECTS IN PETUNIA

1

2

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McQUADE—X-RAY EFFECTS IN PETUNIA

EXPLANATION OF PLATE 29

1. 20,000 r. Calyx members have given way to petaloid structures. In the flower at left, the smaller petaloid structure subtends an anther. Both flowers and petaloid structures show characteristic spotting. About natural size.

2. 20,000 r. Globose. × about ½.

3. 25,800 r. Abundance of weak leaders. × about ½.

4. 16,200 r. Partial development and distortion of flowers. × about ¾.

5. 17,400 r. Fasciated stem. × about ½.

6. ♀ 3,000 r. White flecking of flowers. × about ¼.

EXPLANATION OF PLATE 30

1. 20,000 r (Plant 23). Free-hand section through adjacent light and dark areas on leaf surface (see pl. 28, fig. 1). The thin area at left is a light spot on the leaf. × about 200.

2. 18,000 r (Plant 29). Section through a dark area of leaf where palisade and spongy mesophylls are recognizable. × about 70.

3. 18,000 r (Plant 29). Section through light spot of same leaf shown in fig. 2. × about 70.

4. 20,000 r (Plant 78). Palisade cells squat rather than columnar. × about 70.

5. 25,800 r (Plant 26). Curvature of leaf brought about through difference in development of upper and lower epidermal layers. Mesophyll cells tend to be homogeneous. × about 25.

6. 20,000 r (Plant 40). Homogeneous mesophyll. × about 70.

7. 25,800 r (Plant 26). Detail of fig. 5. Note development of upper as opposed to lower epidermis. × about 35.

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SOME LICHENS OF TROPICAL AFRICA

CARROLL WILLIAM DODGE

The following account is based largely upon two collections from Nigeria and Cameroons by C. A. Thorold; from Sierra Leone by F. C. Deighton and others, and from Uganda on orchid roots by H. A. Omastin (sent by Sir Edward Salisbury, Royal Botanic Gardens, Kew); one from Nyasaland by L. J. Brass (Vernay Expedition to Nyasaland) sent by the New York Botanical Garden; and a few from other sources.

Using Zahlbruckner's *Catalogus Lichenum Universalis* and other sources, in all the genera represented, I made keys to the species described from tropical Africa, here defined as the area between 15° N. and 15° S. latitudes and between 20° W. and 55° E. longitudes, but including all of Mozambique and Nyasaland in the east and Angola in the west. I also included the neighboring islands: the Cormoro Archipelago and Socotra, off the east coast, and Ascension, St. Helena, São Thomé, Annobon, Ilha Principe, and Fernando Po, off the west coast. Unfortunately, I have not had access to Stirton's papers in the *Transactions of the Glasgow Society of Field Naturalists*, which may have included some species from this area. I am including these keys at the appropriate places in hope that they may be useful to other lichenologists who may study material from this area. The countries and islands mentioned in the keys are those from which the species were described and do not indicate the geographic distribution of the species in question.

Perhaps the most interesting results are from Acharian species based on the collections of Afzelius in 1792-94 from Sierra Leone and Guinea. I have been unable to locate information regarding Afzelius' journey, but assume his "Guinea" was the Guinea Coast proper of geographers of that time, which included the modern Gold and Ivory Coasts although it may have included the whole coast from Senegal to Nigeria. The Nigerian and Cameroons collections are interesting as wholly collected on the bark of *Theobroma* (the foliicolous species having been sent to Santesson and published in his *Foliicolous Lichens I* (Symb. Bot. Upsal. 12:1:1–590. 1952). I know of no other such extensive collections from the bark of a single species of tree. In contrast to my experience with collecting on this substrate in Central America, *Leptogium* is represented by a few unidentifiable scraps, and the Pannariaceae are absent, both the most conspicuous groups in Central America. Below is a list of the species found on *Theobroma:*

PYRENULACEAE

Pyrenula eucalypta Vainio
Pyrenula fuscolurida Vainio
Pyrenula heteroclita Ach.
Pyrenula mamillana (Ach.) Trev.
Pyrenula trombetana Vainio
Anthracothecium nigeriensis Dodge

TRYPETHELIACEAE

Melanotheca cameroonensis Dodge
Melanotheca nigeriensis Dodge
Laurera nigeriensis Dodge

ASTEROTHELIACEAE

Pyrenastrum parathelioides Dodge

Issued December 18, 1953.

CYPHELIACEAE

Tylophoron ascidioides Vainio

CRYPTOTHECIEAE

Cryptothecia nigeriensis Dodge
Cryptothecia Thoroldi Dodge

OPEGRAPHACEAE

Opegrapha nigeriensis Dodge
Opegrapha prosodea Ach.

GRAPHIDACEAE

Graphis nigeriensis Dodge
Graphis ondensis Dodge
Graphis Thoroldi Dodge
Phaeographis lynceodes (Nyl.) Zahlbr.
Phaeographis ochracea Dodge
Graphina ulcerata (Vainio) Zahlbr.
Phaeographina deducta (Nyl.) Zahlbr.

CHIODECTONACEAE

Sarcographa labyrinthica (Ach.) Müll. Arg.
Sarcographa Thoroldi Dodge

THELOTREMACEAE

Ocellularia cavata (Ach.) Müll. Arg.
Ocellularia scolecospora Dodge
Ocellularia trypanea (Ach.) Dodge
Thelotrema cameroonensis Dodge
Tremotylium africanum Räs.

COLLEMACEAE

Collema nigrescens var. *minutum* Hue

LECIDEACEAE

Lecidea granifera (Ach.) Vainio
Lecidea nigeriensis Dodge
Lecidea rubina Ach.
Lecidea tenuis Müll. Arg.
Bacidia golungensis (Vainio) Zahlbr.
Bacidia nigeriensis Dodge

PHYLLOPSORACEAE

Phyllopsora Buettneri (Müll. Arg.) Zahlbr.

LECANORACEAE

Lecanora aequinoctialis Stzbgr.

BLASTENIACEAE

Bombyliospora nigeriensis Dodge
Bombyliospora Thoroldi Dodge

PHYSCIACEAE

Physcia Poncinsii Hue

The usual techniques have been employed in this study, and colors have been recorded from Ridgway's *Color Standards and Color Nomenclature*. In some of the Graphidaceae with very thin thalli or where the thallus is endophloeodal, the color recorded may owe nearly as much to the color of the underlying bark as to the thallus, and other colors may be expected if the species is found on barks of other species. In the keys, the colors are those of the original descriptions or those recorded by other lichenologists based on the type specimen.

The data are still too few to warrant subdivision into floras. From the data at hand, it would seem that the East and West African floras are distinct, but little collecting has been done in the central portion of the continent. There is no apparent relation between the flora of North Africa from Morocco to Egypt and that of Sierra Leone. There is a less marked division between Sierra Leone and Liberia, although a few species apparently extend from Sierra Leone all the way to Angola. In the east there seems to be a division between Abyssinia, Somaliland and Socotra island and the area from Kenya southward.

PYRENULACEAE

Thallus crustose, uniform, epi- or endophloeodal; cortex often poorly developed or absent; algae *Trentepohlia;* perithecia solitary in thalline warts, rarely aggregated and somewhat concrescent, but not immersed in a stroma or pseudostroma (distinction from the Trypetheliaceae), erect with a central ostiole; spermatia usually exobasidial.

I have referred here three species of *Polyblastiopsis* and one of *Pseudopyrenula* with a single perithecium in a true stroma. The absence of a pseudostroma has been used to separate this family from the Trypetheliaceae, but it seems likely that when we know more of the development and interrelationships we will com-

bine these families and split on other combinations of characters as suggested by G. T. Johnson (Ann. Mo. Bot. Gard. 27:1–43. 1940). The phylogenetic significance of the stroma has also been questioned in the related Pyrenomycetes (Munk, Dansk Bot. Arkiv 15:2:1–163. 1953).

1. Paraphyses branched and anastomosing, persistent or evanescent....2
1. Paraphyses unbranched and free....6
2. Ascospores unicellular ....*Monoblastia* Riddle
2. Ascospores septate 3
2. Ascospores muriform ....*Polyblastiopsis* Zahlbr.
3. Spore protoplasts cylindric with thin septa....4
3. Spore protoplasts rounded to lenticular....*Pseudopyrenula* Müll. Arg.
4. Spermatia exobasidial or unknown 5
4. Spermatia endobasidial ....*Arthopyreniella* Steiner
5. Ascospores ellipsoid to fusiform....*Arthopyrenia* Mass.
5. Ascospores acicular, often helically twisted....*Leptorhapis* Koerb.
6. Ascospores unicellular ....*Coccotrema* Müll. Arg.
6. Ascospores septate 7
6. Ascospores muriform 11
7. Asci with 1–8 ascospores....8
7. Asci with many ascospores ....*Thelopsis* Nyl.
8. Spore protoplasts cylindric, septa thin 9
8. Spore protoplasts rounded to lenticular, brown....*Pyrenula* Ach.
9. Asci soon evanescent, ascospores acicular....*Belonia* Koerb.
9. Asci not soon evanescent 10
10. Ascospores hyaline ....*Porina* Müll. Arg.
10. Ascospores brown ....*Blastodesmia* Mass.
11. Ascospores hyaline, protoplasts appearing cubical....*Clathroporina* Müll. Arg.
11. Ascospores brown, protoplasts rounded to lenticular....*Anthracothecium* Hampe

THELOPSIS

Thelopsis Nyl., Mém. Soc. I. Sci. Nat. Cherbourg 3:194. 1855.

Thelocarpon sect. *Thelopsis* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 149. 1862.

Sychnogonia Körb., Syst. Lich. Germ. 332. 1855.

Holothelis Clements, Gen. Fung. 40. 1909.

Dithelopsis Clements, Gen. Fung. 40. 1909.

Type: *Thelopsis rubella* Nyl. *Sychnogonia,* published the same year, was based on S. *Bayrhoefferi* Zw., usually regarded as a synonym of *T. rubella. Holothelis* was based on *T. flaveola* Arn., as a segregate for the only species with unicellular spores, which may belong in *Thelocarpon* Nyl. *Dithelopsis* was based on *T. subporinella* Nyl. as a segregate with uniseptate spores. *Thelopsis inordinata* from India might equally well have been segregated as it was described with dwarf muriform spores.

Thallus thin, crustose, ecorticate, with *Trentepohlia* algae, often poorly developed. Perithecia sessile, naked or immersed in a thalline wart, wall relatively soft, light-colored to blackening with a central ostiole; paraphyses slender, free, unbranched (disappearing in *T. selenospora* Dodge); asci fusiform to oblong, the wall soon disappearing; ascospores usually long-ellipsoid, unicellular to 6-celled or dwarf-muriform, often surrounded with a thin halo.

Pyrenulaceae with polysporous asci have been assembled in this genus without much regard to other morphologic characters. *Thelocarpon* Nyl. and *Thelococcus*

Nyl. of the Acarosporaceae have the perithecia immersed in thalline warts with very little development of the perithecial wall, branched paraphyses and protococcoid algae. In other characters they seem more closely related to *Thelopsis* than to other members of the Acarosporaceae. *Thelopsis* has been reported mostly from temperate Europe and the Mediterranean basin, with one species in southern California and one in India.

Thelopsis **selenospora** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Amphimas pterocarpoides*, F. C. Deighton M4334C.

Thallus hypophloeodes, filamentis *Trentepohliae* 5–6 μ diametro, cellulis 10–12 μ longis et hyphis tenuibus. Perithecia sphaerica, solitaria vel subaggregata, sessilia in disco thallino stramineo, aspera, 0.4–0.5 mm. diametro, dimidiata; parathecium 70 μ crassitudine, pseudoparenchymaticum, cellulis 6–8 μ diametro subcubicis, obscure brunneis sed non carbonaceis, ostiolo minuto umbilicato, cum cellulis algarum inter hypothecium et cellulas suberaceas corticis; hypothecium lenticulare, 25–30 μ crassitudine, hyphis dense contextum; paraphyses evanescentes; asci oblongi, apicibus non incrassati, polyspori, 65–70 $\times$ 14–16 μ; ascosporae fusiformes vel seleniformes, apicibus acutis, 6-loculares, septis tenuibus, 24 $\times$ 3 μ.

Thallus hypophloeodal except at the base of the perithecia, mostly between the cork layer and the underlying cells of the bark, consisting of *Trentepohlia* filaments and isolated cylindric cells, 10–12 $\times$ 5–6 μ, somewhat deformed by mutual pressure, and slender hyphae. Perithecia solitary to somewhat aggregated, each sessile on a thin disc of stramineous thallus, surface rough with a minute, inconspicuous ostiole about 0.4–0.5 mm. in diameter, dimidiate (appearing entire in thick sections since the walls of the cork cells at the base are darkened); wall about 70 μ thick, pseudoparenchymatous, cells 6–8 μ in diameter, appearing almost cubical, very dark brown but not brittle and carbonaceous, base with algal cells between the hypothecium and the cork cells of the bark; hypothecium lenticular, about 25–30 μ thick, of densely woven hyphae; paraphyses early disappearing; asci oblong, tip not thickened, polysporous, 65–70 $\times$ 14–16 μ; ascospores fusiform to more commonly crescent-shaped, helically twisted in the ascus as in *Bacidia* subg. *Scoliciosporum*, ends very acute, predominantly 6-locular, septa very thin, protoplasts nearly cylindric, surrounded by a thin halo, about 24 $\times$ 3 μ. Often one end of the ascospore is prolonged as a short filamentous appendage as in the ascospores of the Ashbyaceae.

Except for the polysporous asci and evanescent paraphyses, this species might easily be mistaken for a member of *Arthopyrenia* sect. *Pseudosagedia*. The much darker perithecial wall, evanescent paraphyses, and long-fusiform to crescent-shaped spores easily separate this species from other described species of *Thelopsis*.

POLYBLASTIOPSIS

Polyblastiopsis Zahlbr., in Engler & Prantl, Die nat. Pflanzenfam. I. 1*:67. 1903.
Polyblastia Müll. Arg., Flora 65:401. 1882, *non* Lönnr. 1858.
Mycoglaena Höhnel, Sitzungsber. K. Akad. Wiss. Wien, math. naturw. Kl. 118:1210. 1903.

Type: Thirteen species listed, none designated as type. *Mycoglaena* was based on *Verrucaria subcaerulescens* Nyl.

Thallus crustose, endo- or epiphloeodal; perithecia solitary, nude or more or less covered by the thallus, hemispheric or spherical, ostiole central; paraphyses branched and anastomosing; asci 1–8-spored; ascospores ellipsoidal to fusiform, muriform, septa thin, with or without a halo, hyaline.

Polyblastiopsis differs from *Clathroporina* only in the branched and anastomosing paraphyses instead of unbranched and free. It may also be confused with *Laurera* of the Trypetheliaceae when the perithecia are crowded. A monograph of the whole group is badly needed.

The systematic position of the species referred here is uncertain. While, in general, the perithecia occur singly, occasionally 2–3 are concrescent, often of quite unequal age, as if a new perithecium started to expand near the base of an older perithecium and the outer portions of the "walls" grew together. A strict morphologic interpretation of the perithecial wall would limit it to the inner carbonaceous wall, and the rest true stromatal tissue, especially since spermogonia occur in it. We have essentially monoperithecial stromata. Such an interpretation would place these species in *Laurera* in a special section, since the species previously described have several perithecia in each stroma. We have the same situation in *Pseudopyrenula Deightoni* Dodge in relation to *Bathelium*. On the other hand, most lichenologists, not being specialists in the Pyrenomycetes, would probably overlook the distinction and look for these species where I have placed them. It is hoped that comparative studies of the development of many more species in both the Pyrenulaceae and Trypetheliaceae, will eventually place our classification on a sounder basis.

1. Ascospores 4 per ascus, 190–220 × 30 μ; perithecium entire; Angola.....*P. fulva* (Vainio) Dodge
1. Ascospores 8 per ascus.....2
   2. Ascospores 20–34(–40) × 11–13 μ, 14–16-locular, 6-locellate; perithecium entire, occurring singly in a thick stroma; Sierra Leone .....*P. pyriformis* Dodge
   2. Ascospores 25–28 × 10 μ, 6–8-locular, 2–4-locellate; perithecium dimidiate; Socotra .....*P. tropica* (Müll. Agr.) Zahlbr.
   2. Ascospores more than 75 μ long; perithecium entire.....3
3. Ascospores (75–)80(–85) × 14–16 μ, 14-locular, 2–3-locellate; perithecium thin, occurring singly in a thick stroma; Sierra Leone.....*P. linearis* Dodge
3. Ascospores (80–)100–120(–126) × 18–26 μ, 32–36-locular, plurilocellate, perithecium 120–140 μ thick on the sides, 20–30 μ thick at the base; Congo.....*P. haematochroa* Hue
3. Ascospores 133–160 × 27 μ, 24-locular, 8-locellate; perithecium 50–55 μ thick, occurring singly in a spherical stroma; Sierra Leone.....*P. sphaerica* Dodge

Polyblastiopsis fulva Dodge, comb. nov.

Thelenella (Euthelenella sect. *Microglaena) fulva* Vainio, Cat. Welwitsch Afric. Pl. 2:451. 1901.

Clathroporina fulva Zahlbr., Cat. Lich. Univ. 1:418. 1922.

Type: Angola, Golungo Alto, near Mata Quisuculo, on wild *Citrus medica*, Welwitsch 230.

Zahlbruckner was in error in transferring this species to *Clathroporina*, as Vainio clearly states that the paraphyses are branched and anastomosing, the main character differentiating *Polyblastiopsis* from *Clathroporina*.

POLYBLASTIOPSIS **pyriformis** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on trunk of *Anisophyllea laurina*, F. C. Deighton M4404.

Thallus epiphloeodes, olivaceus, nigro-marginatus, 160 μ crassitudine; cortex 55 μ crassitudine, gelifactus, hyphis tenuibus periclinalibus; stratum algarum 80 μ crassitudine filamentis *Trentepohliae* verticalibus, densis, 6–8 μ diametro, cellulis subrotundatis; medulla 25 μ crassitudine, hyphis tenuissimis. Stromata sessilia, subpyriformia, 0.5 mm. diametro, 0.6 mm. altitudine, basi constricta; cortex stromaticus 15 μ crassitudine, hyphis periclinalibus brunneis, stratum interius pseudoparenchymaticum, 30 μ crassitudine; parathecium carbonaceum, integrum, 30 μ crassitudine; hypothecium lenticulare, centro 40 μ crassitudine; paraphyses tenues, dichotome ramosae anastomosantesque; asci cylindrici, dein subfusiformes, 135 $\times$ 25 μ; ascosporae imbricatim monostichae dein subdistichae, fusiformes, murales, hyalinae, 14–16-loculares, 6-locellatae, 30–34(–40) $\times$ 11–13 μ. Spermatia bacillares, 5–6 $\times$ 1.5 μ.

Thallus epiphloeodal, about 160 μ thick, dark olive buff with a narrow black margin; cortex 55 μ thick, gelified from slender periclinal hyphae; algal layer 80 μ thick, of vertical, closely packed filaments of *Trentepohlia* 6–8 μ in diameter, cells somewhat rounded; medulla about 25 μ thick, of very slender, densely woven hyphae, extending some distance farther into the bark cells. Stromata sessile, subpyriform, about 0.5 mm. in diameter, 0.6 mm. tall, constricted at the base; cortex 15 μ thick, brownish, of relatively large periclinal hyphae, interior pseudoparenchymatous, about 30 μ thick; parathecium carbonaceous, entire, 30 μ thick; hypothecium lenticular, about 40 μ thick in the center; paraphyses slender, dichotomously branched and anastomosing in the nuclear gel; asci cylindric at first, becoming subfusiform with a rounded tip, about 135 $\times$ 25 μ; ascospores imbricately monostichous, becoming subdistichous, fusiform, muriform, hyaline, about 14–16-locular, 6-locellate, protoplasts very slightly rounded, 30–34(–40) $\times$ 11–13 μ.

Spermogonia too old for satisfactory description, arising in the base of the young stroma near the perithecial initial, becoming distorted and flattened against the stromatal cortex as the perithecium expands; wall hyaline or nearly so; spermatiophores not clearly seen; spermatia bacilliform, 5–6 $\times$ 1.5 μ.

Sierra Leone: Njala (Kori), on *Anisophyllea laurina*, F. C. Deighton M4404, type; on *Dialium guineense*, F. C. Deighton M4794.

POLYBLASTIOPSIS **linearis** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Citrus aurantifolius*, F. C. Deighton M4634.

Thallus epiphloeodes, olivaceus, subverrucosus, non nigro-marginatus, 200 μ crassitudine; cortex 40 μ crassitudine, gelifactus; stratum algarum 90–100 μ crassitudine filamentis *Trentepohliae* verticalibus 8 μ diametro, cellulis ad 16 μ longitudine; medulla 65 μ crassitudine, hyphis tenuibus. Stromata linealiter disposita sed rare concrescentia, sessilia, nuda, subsphaerica, basi constricta, nigra, 1.25–

1,3 mm. diametro; cortex stromaticus 15 μ crassitudine, hyphis pachydermeis intertextis, obscure brunneis; stratum interior 90–100 μ crassitudine, pseudoparenchymatica ex hyphis periclinalibus 5 μ diametro; parathecium 20–25 μ crassitudine, integrum, carbonaceum; nucleus sphaericus vel subpyriformis, circa 1000 μ diametro; hypothecium 30 μ crassitudine; paraphyses tenues ramosae anastomosantesque; asci cylindrici, pachydermei (ad 18 μ crassitudine), dein leptodermei (3–4 μ), stipes ad 130 μ longitudine, tenuis, venter 510 $\times$ 40 μ; ascosporae octonae, imbricatim distichae, hyalinae, murales, fusiformes, 14-loculares, 2–3-locellati, (75–) 80 (–85) $\times$ 14–16 μ, tenui cum halone juventute indutae.

Thallus epiphloeodal, citrine drab to deep olive, somewhat verrucose, not black-margined, about 200 μ thick; cortex 40 μ thick, gelified from subvertical hyphae; algal layer 90–100 μ thick, of vertical filaments of *Trentepohlia* 8 μ in diameter, cells about 16 μ long, the upper surface of the layer quite uneven; medulla 65 μ thick, of densely woven slender hyphae with occasional bark cells; some of the algal filaments penetrating into the bark and forming 2–3 thin layers of thallus between the layers of bark cells. Stromata often closely aggregated in lines but rarely concrescent, sessile, subspherical, nude, very constricted at the base, black, 1.25–1.3 mm. in diameter; stromatal cortex 15 μ thick, of dark brown, thick-walled interwoven hyphae with lacunae (probably from old spermogonia); interior 90–100 μ thick, of brown, relatively thin-walled pseudoparenchyma from periclinal hyphae about 5 μ in diameter; parathecium 20–25 μ thick, entire, carbonaceous; nucleus spherical to subpyriform, about 1000 μ in diameter; hypothecium about 30 μ thick, covering the base of the parathecium; paraphyses slender, branching and anastomosing; asci cylindric and very thick-walled (18 μ) when young, becoming more fusiform and thin-walled (3–4 μ) at maturity, 8-spored, stipe about 130 μ long, slender, venter about 510 $\times$ 40 μ; ascospores imbricately subdistichous, hyaline, muriform, fusiform, about 14-locular, 2–3-locellate, with a thin halo when young, (75–) 80 (–85) $\times$ 14–16 μ.

POLYBLASTIOPSIS **sphaerica** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Orthocosmus africanus*, F. C. Deighton M4795.

Thallus epiphloeodes, ochraceo-olivaceus, margine tenui, nigro, 100–110 μ crassitudine; cortex 40 μ crassitudine, gelifactus hyphis periclinalibus; stratum algarum 25–30 μ crassitudine, filamentis verticalibus *Trentepohliae*, 10–11 μ diametro; medulla 40–45 μ crassitudine, hyphis tenuibus dense contexta. Stromata 1–1.5 mm. diametro, subsphaerica, sessilia, basi constricta, ostiolo subumbilicato; cortex 30 μ crassitudine, hyphis periclinalibus obscure brunneis; stratum interius 90–95 μ crassitudine, pseudoparenchymaticum obscure brunneum; parathecium 50–55 μ crassitudine, integrum, carbonaceum; nucleus subpyriformis, gelifactus; hypothecium 40 μ crassitudine hyphis tenuibus dense contextum; paraphyses tenues, ramosae anastomosantesque; asci pachydermei, cylindrici juventute, dein clavati, leptodermei, stipite tenui, 50 μ longitudine, venter 300 $\times$ 50–55 μ; ascosporae octonae, subdistichae, hyalinae, murales, 24-loculares, 8-locellatae, halone tenui indutae, 133–160 $\times$ 27 μ.

Thallus epiphloeodal, between olive ochre and ecru-olive, with a very narrow black margin, 100–110 μ thick; cortex about 40 μ thick, gelified from predominantly periclinal hyphae; algal layer about 25–30 μ thick, of vertical filaments of *Trentepohlia* 10–11 μ in diameter, upper surface very uneven; medulla 40–45 μ thick, of densely woven slender hyphae, including many disorganized bark cells. Stromata 1–1.5 mm. in diameter, subspherical, sessile, constricted at the base, with a slight depression about the ostiole; cortex about 30 μ thick, of periclinal dark brown hyphae; interior 90–95 μ thick, of dark brown thin-walled pseudoparenchyma (black in thick sections with lacunae probably from old spermogonia); parathecium 50–55 μ thick, entire, carbonaceous; nucleus highly gelified, subpyriform; hypothecium 40 μ thick, of slender, densely woven hyphae covering the base of the parathecium; paraphyses slender, branched and anastomosing; asci 8-spored, very thick-walled and cylindric at first, becoming thin-walled and clavate as the spores mature, stipe slender, about 50 μ long, venter about 300 $\times$ 50–55 μ; ascospores subdistichous, hyaline, muriform, about 24-locular, 8-locellate, with a thin halo, 133–160 $\times$ 27 μ.

Deighton M4649 has smaller ascospores (93–) 133 (–146) $\times$ (19–) 21 μ and a grayer thallus, i.e. citrine-drab to deep olive, but is otherwise similar in structure.

Sierra Leone: Njala (Kori), on bark of *Orthocosmus africanus*, F. C. Deighton M4795, type; on bark of *Dialium Dinklagii*, F. C. Deighton M4649.

PSEUDOPYRENULA

Pseudopyrenula Müll. Arg., Flora 66:247. 1883.

Type: none designated, 17 species listed. *Pyrenula pupula* Ach. should be chosen as the type, since it belongs in the section with the largr number of species.

Thallus crustose, epi- or endophloeodal with *Trentepohlia* algae. Perithecia entire or dimidiate, wall carbonaceous, nude or partly covered by the thallus; paraphyses branched and sometimes anastomosing; asci 8-spored; ascospores hyaline, transversely septate, protoplasts rounded, not cylindric.

This genus is analogous to *Pyrenula*, being segregated for its hyaline spores. It differs from *Porina* Müll. Arg. in its branched paraphyses and the rounded or lenticular protoplasts of its ascospores. In a few species, the perithecia tend to be aggregated but not assembled in a definite pseudostroma as in *Bathelium* and *Trypethelium*. It is widely distributed in the tropics but less common than *Pyrenula* in most floras.

1. Perithecium entire 2
1. Perithecium dimidiate, ascospores 4-locular 4
   2. Ascospores 4-locular 3
   2. Ascospores 6–8-locular, 16–22 $\times$ 6–7 μ; perithecial warts hemispheric, black, 0.3–0.35 mm. in diameter; Mozambique ..... *P. polyphragmia* Vainio
3. Ascospores 22–27 $\times$ 7–9 μ; perithecial wart 0.5 mm. in diameter; São Thome ..... *P. infossa* (Nyl.) Zahlbr.
3. Ascospores 18–21 $\times$ 6–8 μ; peritheca very thin-walled, solitary in a brown stroma, ostiole surrounded by a white disc; Sierra Leone ..... *P. Deightoni* Dodge
   4. Ascospores 16–20 $\times$ 4–6 μ; thallus whitish; Angola ..... *P. bengoana* Vainio
   4. Ascospores 23–24 $\times$ 5.5–6 μ; thallus olivaceous; Angola ..... *P. conica* Müll. Arg.

SECT. HOMALOTHECIUM

PSEUDOPYRENULA sect. HOMALOTHECIUM Müll. Arg., Bot. Jahrb. [Engler] 6:408. 9 June, 1885.

Pseudopyrenula sect. *Holothecium* Müll. Arg., Flora 68:331. 11 June 1885.

Section *Homalothecium* was formally described, limiting the group to species with immersed, entire perithecia, listing *Pyrenula annularis* Fée, *P. neglecta* Müll. Arg., *P. discolor* and *P. discolorella*. Section *Holothecium* was proposed without formal description, treating *P. annularis* Fée, *P. porinoides* Müll. Arg., *P. Pupula* Ach., and *P. neglecta* Müll. Arg., evidently intended for species with entire perithecia. In 1888 (Mém. Soc. Phys. Hist. Nat. Genève 30:3:28–29), Müller Argau did not use section names, although he treated two species under the heading "Perithecium completum," *P. Pupula* (about one-third emersed) and *P. ceratina* (Fée) Müll. Arg. (more innate). Zahlbruckner (in Engler, and Die nat. Pflanzenfam. 8:78. 1926) limits the section with 4-celled spores, listing *P. Pupula* (Ach.) Müll. Arg. and *P. annularis* (Fée) Müll. Arg.

PSEUDOPYRENULA **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Peltophorum africanum* var. *speciosum*, F. C. Deighton M4340.

Thallus epiphloeodes, isabellinus vel brunneo-olivaceus, margine nigro; cortex 55 μ crassitudine, decompositus; stratum algarum 30–60 μ crassitudine, filamentis verticalibus *Trentepohliae*, 5–6 μ diametro, cellulis 8 μ longitudine; medulla 80–160 μ crassitudine, hyphis tenuibus dense contexta. Stromata 0.5 mm. diametro, 0.3 mm. altitudine, sessilia, nuda, nigra, ostiolo albo-marginato, 70–80 μ crassitudine, pseudoparenchymatica, brunnea, cellulis 5–6 μ diametro; parathecium 5–6 μ crassitudine, integrum, carbonaceum; hypothecium 10 μ crassitudine, hyalinum, hyphis tenuibus pachydermeis dense contextum; paraphyses 130–150 μ altitudine, dichotome ramosae; asci cylindrici, apice non incrassati, 100 × 14 μ; ascosporae octonae, imbricatim distichae, ellipsoideae, 4-loculares, protoplastis rotundatis, 5–6 μ diametro, juventute cum halone, 18–21 × 6–8 μ.

Thallus epiphloeodal, isabelline to light brownish olive or darker, with a conspicuous black margin; cortex about 55 μ thick, decomposed; algal layer 30–60 μ thick, of vertical filaments of *Trentepohlia* 5–6 μ in diameter, cells about 8 μ long; medulla 80–160 μ thick, of slender, densely woven hyphae containing disintegrating bark cells and an occasional algal cell. Stromata about 0.5 mm. in diameter and 0.3 mm. tall, each containing a single perithecium, sessile, nude, black except for the whitish disc about the ostiole; wall about 70 μ thick on top and sides of the perithecium, 80 μ thick below it, of brown, coarse hyphae forming a pseudoparenchyma with isodiametric cells 5–6 μ in diameter; parathecium very thin, 5–6 μ, black, carbonaceous, entire; hypothecium about 10 μ thick, hyaline, of densely woven, thick-walled hyphae; paraphyses 130–150 μ tall, sparingly dichotomously branched, imbedded in the nuclear gel; asci cylindric, 8-spored, about

100 × 14 μ, tip not thickened; ascospores imbricately distichous, ellipsoidal, 4-locular, protoplasts spherical, 5–6 μ in diameter, with a conspicuous halo 3 μ thick when young, 18–21 × 6–8 μ.

This species is related to *P. infossa* (Nyl.) Zahlbr. from São Thomé, from which it is distinguished by the white disc about the ostiole, the more emergent and smaller "perithecia," and smaller spores. The systematic position of this species is uncertain. I have placed it in *Pseudopyrenula* because of the hyaline spores and the perithecia solitary in the stroma, but a strictly morphologic interpretation would place it in *Bathelium*, which usually has several perithecia per stroma. The distinction between the parathecium and stromatal tissue is clear only in very thin sections. It is analogous to the species which I have placed in *Polyblastiopsis* in their relation to *Laurera*.

Sierra Leone: Njala (Kori), on bark of *Peltophorum africanum* var. *speciosum*, F. C. Deighton M4340, type; on *Citrus aurantifolius*, F. C. Deighton M4627.

Sect. Hemithecium

Pseudopyrenula sect. Hemithecium Müll. Arg., Bot. Jahrb. [Engler] 6:407. 1885.

Type: not designated; *P. flavicans* Müll. Arg., *P. diremta* (Nyl.) Müll. Arg., *P. diluta* (Nyl.) Müll. Arg., *P. subgregaria* Müll. Arg., *P. superans* Müll. Arg., and *P. elliptica* were listed.

Perithecia dimidiate or base very thin, sessile or slightly immersed at the base, nude, conico-hemispheric; spores 4-locular.

Pseudopyrenula bengoana Vainio, Cat. Welwitsch Afric. Pl. 2:457. 1901.

Type: Angola, Bengo near Quifandongo, on twigs, *Welwitsch 437*.

Thallus epiphloeodal, thin, whitish, smooth, surface dull, without a distinct hypothallus or partly with a black margin, K—. Perithecia solitary, hemispheric, 0.2–0.25 mm. in diameter, nude, black or with a slight thalline covering at the base, ostiole slightly impressed; wall dimidiate, fuliginous; paraphyses branched and anastomosing; asci 8-spored, subcylindric, 40 × 12 μ; ascospores distichous, oblong, hyaline, 4-locular, protoplasts lenticular, equal, 16–20 × 4–6 μ.

Our specimen has a deep olive-buff thallus with a complete and conspicuous black margin; the asci are about 50–55 × 10–12 μ, ascospores 20–22 × 5–6 μ with spherical protoplasts 5 μ in diameter. In other characters it agrees well with Vainio's description translated above. Since I have not seen the type, I have preferred to refer my material to Vainio's species rather than describe it as new.

Sierra Leone: Njala (Kori), on *Peltophorum africanum* var. *speciosum*, F. C. Deighton M4341, M4343.

PYRENULA

Pyrenula Ach., Lichenogr. Univ. 64–66, 314–318, 676. 1810, *pro parte minore*; Mass., Ricerche Autonom. Lich. Crost. 162. 1852.

Bunodea Mass., Symmicta, 74. 1855.

Type: The selection of the type is very difficult. Of the nine species treated

by Acharius in 1810, seven have been transferred elsewhere and the two remaining species, *P. ocellata* and *P. subaperta*, have not been studied microscopically, hence their systematic position is uncertain. Massalongo, in 1852, was the first to use microscopic characters in the modern sense, and in 1855 he designated *P. Alni* Mass. as the type and *P. nitida* (Weig.) Ach. (1814) as the type of his segregate *Bunodea*. Koerber (Syst. Lich. Germ. 359. 1855) suggested that *P. nitida* differed from the other species which he included in the genus and might be taken as the type of a new genus, although he did not propose one. He abandoned the idea later, reducing *Bunodea* to synonymy in his *Parerga Lichenologica* 333–334. 1863. Either species would conserve the generic name in its present sense.

Thallus crustose, epi- or endophloeodal, ecorticate, with *Trentepohlia* algae; perithecia solitary or aggregate, nude or immersed in the thallus; wall black, entire or dimidiate; paraphyses simple, free; asci 8-spored; ascospores usually 4-locular (2-locular in sect. *Pseudacrocordia* and 6–10-locular in sect. *Fusidiospora*), brown, with lenticular, round or polyhedral protoplasts.

This genus differs from *Pseudopyrenula* in its brown ascospores, and from *Melanotheca* by the absence of a clearly developed pseudostroma, in which the perithecia are imbedded. The genus is widely distributed in tropical regions with a few species in the temperate zone.

1. Perithecia entire, wholly immersed at maturity except for the ostiolar disc or papilla.....2
1. Perithecia emergent to nearly sessile at maturity.....5
   2. Perithecia flat above, forming a black disc about the ostiole below the level of the greenish thallus, the lower half of the perithecium sunken in the bark; spore size unknown; Sierra Leone .....*P. ocellata* Ach.
   2. Perithecia hemispheric, disc black; thallus greenish ashy becoming cinnabar red; spores 20 × 8 μ; Kenya.....*P. Gravenreuthii* Stein
   2. Perithecia rounded above, often with an ostiolar papilla; spores mostly more than 20 μ long 3
   2. Perithecium spherical; ascospores 23 × 10–12 μ, 4-locular; Socotra....*P. obscurata* Müll. Arg.
3. Base of perithecium thinner than the sides, perithecia 0.7–0.8 mm. in diameter; spores 22–34 × 11–15 μ; thallus pale tawny; Angola.....*P. gibberosa* Vainio
3. Base of perithecium as thick as the sides.....4
   4. Spores 25–34 × 10–14 μ; thallus olive; Kenya.....*P. mastophorizans* Müll. Arg.
   4. Spores (17–)23–24(–29) × 10–13 μ; thallus stramineous; Mozambique....*P. mozambica* Vainio
   4. Spores 17–24 × 9–10 μ; thallus pale olive; perithecia 0.15–0.3 mm. in diameter; Angola .....*P. Euphorbiae* Vainio
5. Spores more than 25 μ long; thallus pale.....6
5. Spores less than 20 μ long.....8
   6. Base of perithecium as thick as sides, perithecium subspherical, 0.7–1 mm. in diameter; ascospores 36–42 × 16–18 μ; Angola.....*P. Acaciae* Vainio
   6. Base of perithecium thinner than sides; apical protoplasts of ascospores smaller than the middle ones 7
7. Perithecial warts 0.5–0.6 mm.; perithecium oblate-spheroid but not winged at the base; ascospores (25–)36 × (11–)15 μ; Angola .....*P. trombetana* Vainio
7. Perithecial warts 0.5–0.7 mm.; perithecium oblate-spheroid, winged at the base; ascospores 30–37 × 14–16 μ; Angola.....*P. eucalypta* Vainio
7. Perithecial warts 0.7–0.8 mm.; perithecium spherical; ascospores 30–38 × 12–15 μ; Angola .....*P. oculifera* Vainio
   8. Perithecium dimidiate 9
   8. Perithecium entire 10
9. Perithecia 0.2–0.25 mm.; ascospores 14–16 × 5–6 μ; thallus white; Sierra Leone..... .....*P. parva* Vainio
9. Perithecia 0.5–0.8 mm.; ascospores 14–17 × 6–7 μ; thallus fuscous; Sierra Leone..... .....*P. fuscolurida* Vainio

10. Thallus white or pale ashy; perithecia conic-hemispheric; apical cells of ascospores smaller than middle cells 11
10. Thallus ashy olive; perithecia 0.15–2 mm., flattened-conic, base thinner, winged; ascospores 15–16 × 4.5–5 μ; apical cells not smaller; Guinea..... *P. heteroclita* Ach.
10. Thallus green or yellow-green 12
10. Thallus drab to hair brown; perithecia conic, base winged, 0.6–0.7 mm.; nucleus conic; ostiole umbilicate; ascospores 13–14 × 8 μ, apical cells not conspicuously smaller; Nigeria ..... *Melanotheca nigeriensis* Dodge
11. Perithecia 0.5 mm., with flat base, not winged; ascospores 11–16 × 7–9 μ; thallus whitish, partly black-margined; São Thomé..... *P. glabriuscula* (Nyl.) Vainio
11. Perithecia 0.6–0.8 mm., nucleus spherical; ascospores 13–14 × 5–6 μ; thallus pale ashy; Mozambique ..... *P. Limae* Vainio
12. Perithecia 0.5–0.6 mm., hemispheric with flat base as thick as the sides; ascospores 14–16 × 8–11 μ, apical cells smaller; thallus yellowish-greenish; Sierra Leone ..... *P. aspistea* Afz. in Ach.
12. Perithecia 0.6–0.7 mm., flattened-conic with papilla; ascospores 17–21 × 7–8 μ, apical cells not smaller; thallus green; Sierra Leone..... *P. mamillana* (Ach.) Trev.

PYRENULA TROMBETANA Vainio, Cat. Welwitsch Afric. Pl. 2:454. 1901.

Type: Angola, Golungo Alto, near Trombeta, 330–660 m., on bark of Leguminosae, *Welwitsch 124*.

Thallus epiphloeodal, pale olive buff with a paler inconspicuous margin, about 125 μ thick; cortex 100 μ thick, of very slender, periclinal, conglutinate hyphae, the outer 25 μ somewhat decomposed and granular; algal layer up to 25 μ thick, lying on the outermost bark cells, somewhat discontinuous, of *Trentepohlia* filaments about 6 μ in diameter; medulla not differentiated but fungus hyphae penetrate between the cork cells and disorganize them. Perithecia 0.6–0.8 mm. in diameter, spherical, nearly innate in the bark until the spores mature, then emersed about one half and appearing hemispheric; wall 55 μ thick at the ostiole, expanding to 80 μ at the base, then thinning to about 25 μ under the thecium, carbonaceous, covered with a layer of thalline cortex about 15 μ thick; ostiole somewhat excentric (but not as much so as in *Parathelium*), somewhat umbilicate and paler in old perithecia before the upper half cracks away, first exposing the nuclear remains, then leaving a cupuliform depression; hypothecium scarcely developed; paraphyses slender, dichotomously branched in the thecial gel; asci cylindric, thin-walled, about 135 × 20 μ, the wall disappearing before the ascospores mature; ascospores monostichous, broadly ellipsoidal, fuscous, 4-locular, apical protoplasts hemispheric, about 5 μ in diameter, central spherical to somewhat angled, 8–9 μ in diameter, the whole ascospore 27–32 × 14–16 μ.

The above description is based on our material. Vainio reports the thallus wholly endophloeodal, the perithecia only 0.5–0.6 mm. in diameter, the ascospores distichous and slightly larger (25–) 36 × (11–) 15 μ, with the apical protoplasts only a little smaller. The thalline characters of *P. oculifera* Vainio from Angola are closer to our material but the thallus is abruptly thinned leaving an area 0.3–0.4 mm. about the ostiole and the ascospores are somewhat longer and narrower.

Nigeria: Ondo Province, Owena near Akure, on *Theobroma*, C. A. Thorold 171.

PYRENULA EUCALYPTA Vainio, Cat. Welwitsch Afric. Pl. 2:453. 1901.

Type: Angola, Golungo Alto, near Luinha, on *Ficus Quebeba* Welw., Welwitsch 213 *p.p.*

Thallus epiphloeodal, relatively thick, about 250 μ, pale olive buff; cortex 65 μ thick, gelified, of densely woven, predominantly periclinal, very slender hyphae; algal layer about 30 μ thick, cells short-cylindric, 5–6 μ in diameter, mostly not united in filaments, *Trentepohlia;* medulla about 155 μ thick, of densely woven hyphae, containing occasional disintegrating bark cells and algal cells. Perithecia solitary, immersed in the thallus at first, becoming hemispheric, the lower half covered by thallus and the upper portion by a thin layer of cortex thinning to 10 μ about the ostiole through which the black perithecium shows, and lining the ostiolar depression (about 40 μ thick) which is about 180 μ in diameter, thus appearing white and conspicuous; parathecium about 230 μ thick in the middle of the sides, tapering toward the ostiole and toward the base, not produced into a wing at the base in our material, base thinner, about 125 μ thick, somewhat flattened (but not as flat as in *P. mamillana*), carbonaceous and brittle; hypothecium scarcely developed; paraphyses slender, dichotomously branched, without conspicuous oil droplets in the thecial gel; asci cylindric, 8-spored; ascospores fuscous, 4-locular, ellipsoid, protoplasts square in optical section, the sides of the middle two about 6–8 μ, of the apical ones 5–6 μ, the whole ascospore 30–37 $\times$ 14–16 μ.

Cameroons: Kumba, on *Theobroma,* C. A. Thorold 102.

PYRENULA FUSCOLURIDA Vainio, Cat. Welwitsch Afric. Pl. 2:453. 1901.

Type: Sierra Leone, near Freetown, on *Spondias Mombin* L., Welwitsch 247 *p.p.*

Thallus endophloeodal, indicated by a fuscous or testaceo-fuscous area surrounded by a black line; perithecia solitary or rarely 2–3-confluent, flattened-hemispheric and only slightly emergent until the ascospores mature then becoming hemispheric and empty as the nucleus disintegrates, 0.5 mm. or more in diameter, dimidiate, base angled but not winged; ostiole minute, not surrounded by a papilla; parathecium about 100 μ thick at the base, tapering to about 40 μ thick about the ostiole, carbonaceous, brittle; hypothecium very thin so that the asci and paraphyses appear to arise directly from the somewhat darker bark cells; paraphyses branched, apparently somewhat anastomosed above the asci; asci 8-spored, narrowly cylindric; ascospores obliquely monostichous, 4-locular, protoplasts of about equal size, rounded, fuscous, 14–17 $\times$ 6–7 μ.

Our Nigerian material is very old and the spores are shrunken so that no measurements could be obtained. Our material from Sierra Leone is very young and shows an epiphloeodal citrine thallus 80 μ thick, cortex 25–50 μ thick, of decomposed periclinal hyphae; algal layer 50–75 μ thick, somewhat discontinuous, of more or less disorganized *Trentepohlia* filaments; medulla not differentiated, but fungus hyphae extend between the bark cells and disorganize them. Young perithecia show a thin black wall about 25 μ thick, of very slender periclinal hyphae,

surrounded by a brown pseudoparenchymatous layer 50–70 μ thick, then an algal layer about 50 μ thick, and a cortex 40 μ thick of brownish more slender hyphae with granules. As the perithecium matures, the algae die and disintegrate and the whole darkens into the thick parathecium. Mature ascospores agree in size with those described by Vainio.

Sierra Leone, Njala (Kori), on *Cassia siamea*, F. C. Deighton M4793.

Nigeria: Ondo Province, Aponmu near Akure, on *Theobroma*, C. A. Thorold 172a.

PYRENULA HETEROCLITA Ach., Syn. Lich. 127. 1814.

Type: Guinea, corticole, Afzelius.

Thallus epiphloeodal, about 60 μ thick, ashy olive; cortex 30 μ thick, of slender, conglutinate periclinal hyphae, the outer 10 μ decomposed and granular; algal layer about 30 μ thick with some of the *Trentepohlia* filaments penetrating the bark cells beneath; medulla not differentiated. Perithecia 150–250 μ in diameter, about 150 μ tall, lenticular in opical section, about half emersed at maturity, nude or with remnants of the decomposed cortex, about 5–8 μ thick; parathecium about 50 μ thick above, winged at the base another 50 μ, thinning under the thecium to 25 μ, carbonaceous; hypothecium 10 μ thick, of very slender, densely woven hyphae; paraphyses slender, dichotomous; asci evanescent; ascospores 4-locular, fusiform to ellipsoid, fuscous, apical protoplasts subconic, only slightly smaller than the subspheric central ones, 15–16 $\times$ 4.5–5.5 μ.

The Sierra Leone material has very old perithecia with the thecia disintegrated and only a few shrunken brown ascospores were seen, but such characters as were observable would place it here. The Cameroons material is very scant, only a portion of a thallus growing on *Theobroma* with *P. mamillana* (Ach.) Trev., *Sarcographa labyrinthica* (Ach.) Müll. Arg., and *Phaeographis lynceodes* (Nyl.) Zahlbr. After a study of the type, Müller Argau concluded that the two varieties were growth stages, v. *minuscula* Ach. being the juvenile stage of the mature v. *denigrata* Ach.

Sierra Leone: Sugar Loaf Mt., 650–750 m., on twigs, F. C. Deighton M4441A.

Cameroons: Tombel on *Theobroma*, C. A. Thorold 136, 138.

PYRENULA MAMILLANA (Ach.) Trev., Conspect. Verruc. 13. 1860.

Verrucaria mamillana Ach., Meth. Lich. 120. 1803.

Type: Sierra Leone, corticole, Afzelius.

Thallus epiphloeodal, deep olive buff, about 65 μ thick; cortex 15 μ thick, decomposed, filled with minute granules; medulla 50 μ thick, of slender, compact, periclinal hyphae with *Trentepohlia* filaments and cylindric cells 4–5 μ in diameter, not clearly aggregated as an algal layer. Perithecia solitary, up to 1 mm. in diameter and 0.6 mm. tall, hemispheric with a slight papilla about the ostiole, base flat, surface dull and very minutely and shallowly pitted (seen only under 36$\times$ magnification); parathecium 50 μ thick at the ostiole, rather abruptly thickening to 100 μ and then tapering to 130 μ at the base and prolonged another 130 μ as

wings, thinning to 40–50 μ under the hypothecium, the whole carbonaceous and brittle; hypothecium scarcely differentiated, groups of asci radiating from various points as if produced by different ascogonia; asci cylindric, 8-spored, about 110 × 8–9 μ; paraphyses slender and dichotomously branched, the thecial gel filled with oil droplets; ascospores ellipsoid, fuscous, 4-locular, 17–21 × 7–8 μ, protoplasts rounded, central ones about 3 μ in diameter, apical ones somewhat smaller.

Sierra Leone: Kanema (Nongowa), on *Copaifera copallifera,* F. C. Deighton M5013.

Nigeria: Ojo Province, Iseyin, on *Theobroma,* C. A. Thorold 103.

Cameroons: Tombel, on *Theobroma,* C. A. Thorold 136.

ANTHRACOTHECIUM

ANTHRACOTHECIUM Hampe in Mass., Atti I. R. Ist. Veneto III, 5:330. 1860.

Bottaria sect. *Anthracothecium* Vainio, Etude Lich. Brésil 2:196. 1890.

Type: *A. Doleschalii* Mass.

Thallus uniform, crustose, endo- or epiphloeodal, with *Trentepohlia* algae. Perithecia solitary or sometimes aggregated but not forming a pseudostroma, usually nearly covered by the thallus; parathecium carbonaceous (sect. *Euanthracothecium*) or light-colored with a darkened area about the ostiole (sect. *Porinastrum*), usually entire; paraphyses unbranched and free; asci 1–8-spored; ascospores ellipsoidal, muriform, with rounded protoplasts, brown; spermatia acicular, often curved.

Since *A. euthelium* (Nyl.) Zahlbr. and *A. lugescens* (Nyl.) Zahlbr. were described as having hyaline, muriform spores, they may belong in *Clathroporina* rather than in *Anthracothecium* where Zahlbruckner transferred them.

1. Spores 7–12 × 5–7 μ, dwarf-muriform, 4-locular with the two middle cells divided by a longitudinal septum; Usambara 2
1. Spores less than 100 μ long, muriform 3
1. Spores over 200 μ long, hyaline; São Thomé (perhaps belong in *Clathroporina*) 4
2. Thallus white; perithecia about 0.1 mm. in diameter ..... *A. punctuliforme* Müll. Arg.
2. Thallus orange-yellow; perithecia 0.7 mm. in diameter ..... *A. vitellinum* Müll. Arg.
3. Spores 50–60 × 22–25 μ; thallus ashy, black-margined; Guinea ..... *A. cinerosum* (Ach.) Müll. Arg.
3. Spores 80–95 × 32–35 μ; thallus pale olive buff to smoke gray; perithecia 2.5 mm. in diameter; Ilha Principe ..... *A. guineense* (Nyl.) Zahlbr.
4. Spores 210–230 × 45–75 μ; asci monosporous; perithecia 0.5 mm. in diameter ..... *A. lugescens* (Nyl.) Zahlbr.
4. Spores 275–300 × 25–27 μ, fusiform; asci 8-spored; perithecia 1 mm. in diameter ..... *A. euthelium* (Nyl.) Zahlbr.

ANTHRACOTHECIUM GUINEENSE Zahlbr., Cat. Lich. Univ. 1:462. 1922.

Verrucaria guineensis Nyl., Lich. Insul. Guineens. 36. 1889.

Type: Ilha Principe, at sea-shore, corticole, Quintas.

Thallus epiphloeodal, pale olive buff to smoke gray, about 65 μ thick; cortex 40 μ thick, of slender, conglutinate, periclinal hyphae; algal layer discontinuous, up to 25 μ thick, cells about 6 μ in diameter, not in distinct filaments and somewhat angular from mutual pressure, *Trentepohlia;* medulla not developed, but the fungus hyphae penetrating deeply into the bark. Perithecia solitary, about 2.5

mm. in diameter, 0.9 mm. tall, covered with a thin layer of thalline cortex to near the ostiole; parathecium 125 μ thick near the ostiole, expanding to 600 μ thick at the base, 125 μ thick under the hypothecium, carbonaceous, with a very dense inner layer about 125 μ thick next the nucleus, the rest of thick-walled pseudoparenchyma with occasional small cavities (remains of old spermogonia?); nucleus subspherical, becoming conic in very old perithecia, 1200–1300 μ in diameter; hypothecium 50 μ thick, of densely woven, deeply staining, slender hyphae; paraphyses slender, dichotomously branched in the thecial gel; asci cylindric, disappearing before the spores mature; ascospores brown, broadly ellipsoid, 14-locular, 8-locellate, 80–95 × 32–35 μ.

The relation of this species to *A. cinerosum* (Ach.) Müll. Arg. is not clear. It agrees in most characters with Müller Argau's description of the Acharian type except in spore size. Ascospores, already free of the ascus and just beginning to assume the smoky color of immature brown spores, fall within the measurements given for *A. cinerosum*. They apparently increase in size at the expense of the thecial gel as they mature and become dark brown. If Müller Argau measured such spores and failed to find the very dark brown mature spores, *A. guineensis* may be a synonym of *A. cinerosum* (Ach.) Müll. Arg. I referred my material to the latter species before I found the very dark brown spores in another perithecium on the same thallus. Only a developmental study of these species can settle the synonymy. Sections of one "perithecium" of *Thorold 104* show two perithecia concrescent with a common wall and ostiole, and might be mistaken for *Parmentaria Chevalieri* Bouly de Lesdain.

Nigeria: on *Theobroma*, C. A. Thorold 104; Aponmu near Akure, on *Theobroma*, C. A. Thorold 172.

TRYPETHELIACEAE

Thallus crustose, uniform, epi- or endophloeodal; ecorticate or corticate (never pseudoparenchymatous); algae *Trentepohlia;* several perithecia (rarely only 1 or 2) immersed in each well-developed pseudostroma, erect, with central, individual ostiole; spermatia exobasidial.

1. Ascospores hyaline 2
1. Ascospores brown 5
   2. Ascospores unicellular ..... *Riddlea* Dodge
   2. Ascospores septate, usually 4- or more celled 3
   2. Ascospores muriform ..... *Laurera* Reichb.
3. Ascospores thin-walled, protoplasts cylindric or nearly so ..... *Tomasellia* Mass.
3. Ascospores thick-walled, protoplasts rounded or lenticular 4
   4. Ascospores 2–4-locular, small ..... *Bathelium* Ach.
   4. Ascospores 6–many-locular, large ..... *Trypethelium* Sprgl.
5. Ascospores septate, usually 4 or more celled, protoplasts rounded or lenticular ..... *Melanotheca* Fée
5. Ascospores muriform ..... *Bottaria* Mass.

RIDDLEA

Riddlea Dodge, gen. nov.

Type: *R. papillosa* Dodge.

Thallus crustosus, epiphloeodes; cortex decompositus; algae *Trentepohlia.* Pseudostromata carnea; perithecia immersa, integra; hypothecia in pulvinulis lenticularibus, plura in quovis perithecio; paraphyses dichotome ramosae anastomosantesque; asci longe stipitati; ascosporae octonae, hyalinae, fusiformes, uniloculares; spermogonia in verrucis thallinis immersa; perifulcrum nigrum; spermatiophorae ampullaceae; spermatia acicularia, recta.

Thallus epiphloeodal, sometimes separating from the bark and appearing subfoliose, but without a lower cortex; cortex decomposed; algae *Trentepohlia.* Pseudostromata soft and fleshy, thalline when young, the algae finally dying and leaving lacunae, variable in shape; perithecia immersed in the pseudostroma, ostioles central; parathecium black; several hypothecia per perithecium, lenticular; paraphyses dichotomously branched and anastomosing; asci long-stipitate, very thick-walled when young, the wall thinning as the ascospores mature, 8-spored; ascospores hyaline, fusiform, unilocular; spermogonia immersed in thalline warts, wall black; spermatothecium folded into labyrinthiform cavities; spermatiophores flask-shaped; spermatia acicular, straight, relatively short.

The fungus component of this genus does not seem closely related to other lichen-forming fungi. The placenta-like cushions from which the long-stalked asci radiate are suggestive of the Coronophorales, but true paraphyses are present and the pseudostroma is quite different. Although the pseudostroma is essentially thalline (i.e. containing algae), it shows little relation to *Coccotrema,* which perhaps belongs in the Pertusariaceae (close to or the same as *Perforaria*) rather than in the Pyrenulaceae. For the present we include *Riddlea* in the Trypetheliaceae, analogous to *Monoblastia* of the Pyrenulaceae, although the relationship does not seem close.

I take pleasure in dedicating this genus to my late friend, Professor Lincoln W. Riddle of Harvard University, who first described *Monoblastia.*

Riddlea **papillosa** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Anisophyllea laurina,* F. C. Deighton M4624.

Thallus epiphloeodes, pallide flavo-olivaceus, 75 μ crassitudine; cortex 10 μ crassitudine, decompositus, minutis cum granulis obscuris; stratum algarum 65 μ crassitudine, filamentis verticalibus *Trentepohliae,* 6.5 μ diametro, cellulis cylindricis isodiametricis, dense compactis; medulla non evoluta. Pseudostromata carnea, thallina cum cellulis algarum inter perithecia morientibus, dein lacunata, alia subsphaerica ca. 1 mm. diametro, alia in pulvinulos applanatos 2–3 mm. diametro, alia sublinearia, hyphis hyalinis 2 μ diametro, cortice thallino tecta; perithecia 370 μ diametro, 250 μ altitudine, oblate sphaeroidea, cervice 100 μ longitudine superne tenuescente ad ostiolum parvum in papilla applanata; parathecium in-

tegrum, nigrum, 15 μ crassitudine; hypothecia plura in quovis perithecio, pulvini lenticulares, 135 μ diametro, centro 40 μ crassitudine; paraphyses tenues, dichotome ramosae anastomosantesque, apicibus liberis; asci 200 $\times$ 30 μ, juventute pachydermei, stipitibus 100 $\times$ 5 μ, venter clavatus vel fusiformis, 100 $\times$ 30 μ; ascosporae octonae, distichae, hyalinae, fusiformes, uniloculares, 24–32 $\times$ 8–11 μ, tenui cum halone. Spermogonia in verrucis thallinis immersa, sphaerica, 250 μ diametro; perifulcrum nigrum, 15 μ crassitudine, hyphis tenuibus periclinalibus; spermatothecium plicatum; spermatiophorae ampullaceae, 10 μ longitudine, venter 2 μ diametro, cervice elongato tenuescente; spermatia acicularia recta, ca. 10 $\times$ 1 μ.

Thallus crustose, epiphloeodal, light yellowish olive, about 75 μ thick, sometimes separating from the bark and appearing subfoliose but lacking a lower cortex; upper cortex about 10 μ thick, decomposed, with minute dark granules (appearing black in thick sections); algal layer 65 μ thick, of *Trentepohlia* filaments, vertical, closely packed, cells cylindric, more or less isodiametric, about 6.5 μ in diameter; medulla not differentiated but hyphae penetrate some distance into the bark cells. Pseudostromata soft, fleshy, of thalline tissue, i.e. containing masses of algal cells between the young perithecia, dying and leaving lacunae, very variable in size and shape, some subspherical, about 1 mm. in diameter, others in flattened cushions 2–3 mm. in diameter while others are elongate and sublinear, composed of closely woven hyaline hyphae about 2 μ in diameter, with masses of algal cells between the young perithecia, covered by the thin thalline cortex; perithecia 370 μ in diameter, 250 μ tall, oblate-spheroidal, with a short neck (about 100 μ long), tapering upward to a small ostiole surrounded by a low, broad papilla; parathecium entire, black, 15 μ thick; hypothecia several per perithecium, as lenticular, placenta-like cushions about 135 μ in diameter and 40 μ thick in the center, from which tufts of asci and paraphyses radiate into the thecial gel; paraphyses slender, dichotomously branched and anastomosing, tips free; asci 200 $\times$ 30 μ, very thick-walled when young, the lower half a stipe about 5 μ in diameter, the upper half clavate to fusiform, the wall thinning as the ascospores mature, 8-spored; ascospores distichous, hyaline, fusiform, unilocular, 24–32 $\times$ 8–11 μ, with a thin halo. Spermogonia immersed in thalline warts, about 250 μ in diameter, wall black, 15 μ thick, of slender periclinal hyphae; spermatothecium folded into labyrinthiform cavities; spermatiophores about 10 μ long, flask-shaped with a long tapering neck, venter about 2 μ in diameter; spermatia acicular, straight, about 10 $\times$ 1 μ.

In habit *Riddlea papillosa* suggests BATHELIUM **papillosum** (Ach.) Dodge, comb. nov. (*Trypethelium papillosum* Ach., Syn. Lich. 104. 1814), and I had tentatively referred my material to that species until I found the mature unicellular ascospores, since the ascospores while still in the ascus are about the size of those of *B. papillosum* before the septa are visible.

BATHELIUM

BATHELIUM Ach., Meth. Lich. 111. 1803, *non* Mass. 1860.

Leightonia Trev., Flora 44:19. 1861.

Trypethelium sect. *Bathelium* Müll. Arg., Bot. Jahrb. [Engler] 6:589. 1885.

Pseudopyrenula subg. *Trypethelium* sect. *Bathelium* Vainio, Etude Lich. Brésil 2:206. 1890.

Type: *B. mastoideum* Afzelius in Ach. *Leightonia* was based on *Trypethelium porosum* Ach.

Thallus crustose, epi- or endophloeodal, cortex thin, gelified, algae *Trentepohlia*. Pseudostromata hemispheric or more flattened and irregular; perithecia ellipsoid to spherical, wall entire; asci 8-spored; ascospores hyaline, ellipsoid, 2–4-locular, protoplasts rounded.

1. Pseudostromata often containing a single perithecium; ascospores 20 × 8 μ, apical cells larger than middle cells; Mozambique ..... *B. duplex* f. *simplicius* (Vainio) Dodge
1. Pseudostromata normally containing several perithecia 2
   2. Papillate about the ostiole [papilla sometimes breaking away in very old perithecia]; thallus ashy olive to fuscous 3
   2. Not papillate about the ostiole; thallus white or nearly so 4
   2. Upper part of the pseudostroma breaking away forming an ostiole 250 μ in diameter; thallus deep olive buff; ascospores 19–21 × 8–9 μ, long remaining hyaline but finally brown when fully mature; Sierra Leone ..... *Melanotheca porosa* Dodge
3. Ascospores 18–22 × 7–8 μ; Sierra Leone ..... *B. mastoideum* Ach.
3. Ascospores 20–27 × 8–9 μ; Guinea ..... *B. papillosum* (Ach.) Dodge
   4. Ascospores 20 × 8 μ, with halo; Mozambique ..... *B. compositum* (Vainio) Dodge
   4. Ascospores 28–33 × 9–10 μ; São Thomé ..... *B. subalbens* (Nyl.) Dodge

BATHELIUM MASTOIDEUM Afzelius in Ach., Meth. Lich. 111. 1803.

Trypethelium mastoideum Ach., Lichenogr. Univ. 307. 1810.

Type: Sierra Leone, corticle, Afzelius.

Thallus epiphloeodal, 100 μ thick, deep olive buff, conspicuously black-margined; cortex 55 μ thick, of vertical, slender interwoven hyphae in a gel; algal layer 45 μ thick, of predominantly periclinal hyphae and disorganized filaments of *Trentepohlia* in a gel; medulla not differentiated but hyphae penetrating the underlying bark cells. Pseudostromata hemispheric, confluent into irregular masses containing 1–10 perithecia, fuscous, yellow within at first, blackening and carbonaceous in age, with a low papilla about the ostiole which soon cracks off; parathecium fusing with the stroma; nucleus rounded at first, becoming subconic, 280 μ in diameter at the base, 100 μ at the ostiole and 185 μ tall, the pseudostroma extending 80 μ below the nucleus and resting on the bark cells; hypothecium 12–14 μ thick, of slender, closely woven, predominantly periclinal hyphae; paraphyses dichotomously branched and anastomosing in the nuclear gel, about 150 μ tall; asci fusiform with rounded tips, 8-spored, about 80 × 14–16 μ; ascospores distichous, hyaline, ellipsoid, 4-locular, with large, subequal, rounded protoplasts, 18–22 × 7–8 μ.

Sierra Leone: Njala (Kori), on bark of *Anisophyllea laurina*, F. C. Deighton M4625.

BATHELIUM **compositum** Dodge, comb. nov.

Pseudopyrenula composita Vainio, Bol. Soc. Broter. II, 6:177. 1929.

Trypethelium compositum Zahlbr., Cat. Lich. Univ. 10:101. 1938.

BATHELIUM DUPLEX f. **simplicius** Dodge, comb. nov.
Pseudopyrenula duplex f. *simplicior* Vainio, Bol. Soc. Broter. II, 6:177. 1929.
Trypethelium duplex f. *simplicius* Zahlbr., Cat. Lich. Univ. 10:101. 1938.

BATHELIUM **papillosum** Dodge, comb. nov.
Trypethelium papillosum Ach., Syn. Lich. 104. 1814.

BATHELIUM **porosum** Dodge, comb. nov.
Trypethelium porosum Ach., Syn. Lich. 106. 1814.
Verrucaria porosa Eschw. in Martius, Fl. Brasil. 1:135. 1833.
Leightonia porosa Trev., Flora 44:19. 1861.
Trypethelium Sprengelii v. *porosa* Nyl. in Hue, Nouv. Arch. Mus. [Paris] III, 4:129. 1892.

BATHELIUM **subalbens** Dodge, comb. nov.
Trypethelium subalbens Nyl., Flora 69:178. 1886.

TRYPETHELIUM

TRYPETHELIUM Sprengel, Einleitung in das Studium der kryptogamischen Gewächse, 350. 1804 [often cited as Anleitung zur Kenntniss der Gewächse 3].
Trypethelium sect. *Eutrypethelium* Müll. Arg., Bot. Jahrb. [Engler] 6:393. 1885.
Pseudopyrenula subg. *Trypethelium* sect. *Eutrypethelium* Vainio, Etude Lich. Brésil 2:204. 1890.

Type: *T. Eluteriae* Sprgl.

Thallus crustose, epi- or endophloeodal, cortex gelified, thin; algae *Trentepohlia*. Pseudostromata hemispheric, or flattened and irregular, usually of a different color than the thallus, containing 2 to many perithecia, which are ellipsoidal or spherical, ostiole central, parathecium entire, carbonaceous; paraphyses branched and anastomosing; asci 8-spored; ascospores long-fusiform, hyaline, 6–22-locular, protoplasts rounded.

1. Pseudostromata blood-red, surface pruinose; thallus ashy; ascospores unknown, so perhaps belonging in *Bottaria* or *Melanotheca* which have species with red pseudostromata; Congo ..... *T. coccinatum* Stzbgr.
1. Pseudostromata not blood-red 2
2. Ascospores acicular, 18–22-locular, 56 × 2.5 μ; Nyasaland ..... *T. aciculare* Dodge
2. Ascospores much broader, ellipsoid to fusiform 3
3. Ascospores 6–8-locular, 188 × 42 μ; thallus and pseudostromata olive-glaucescent; Angola ..... *T. pustulatum* (Vainio) Zahlbr.
3. Ascospores 10–14-locular 4
3. Ascospores 16–18-locular, 85–110 × 15–18 μ; ostioles white; São Thomé ..... *T. leucostomum* (Nyl.) Dodge
4. Ascospores 10–14-locular, 55 × 14 μ; thallus olive ochre; pseudostromata yellow ochre, dark fuscous within, 0.5 mm. tall, elongate and irregular; Guinea ..... *T. anomalum* Ach.
4. Ascospores 14-locular, 80–85 × 14–18 μ; thallus pale, sulfur-pruinose; pseudostromata 1 mm. tall, subspheric, finally black with 2–6 perithecia; Angola ..... *T. sphaerocephalum* (Vainio) Zahlbr.

TRYPETHELIUM **aciculare** Dodge, sp. nov.

Type: Nyasaland, Kasungu Hill, 1100 m., corticole, L. J. Brass 17458a.

Thallus epiphloeodes, glaber, subrimulosus, 135 μ crassitudine, olivaceus, margine plumoso, 3 mm. latitudine, homoeomerus; filamentis *Trentepohliae* plus minusve verticalibus, 6–8 μ diametro. Pseudostromata thallina, pulvinata, irregulariter rotundata, 1 mm. diametro, cum 12–20 peritheciis; perithecia ellipsoidea; parathecium integrum, 12–15 μ crassitudine, pseudoparenchymaticum, ex hyphis periclinalibus superne obscurum, inferne hyalinum; hypothecium non bene evolutum; paraphyses dichotome ramosae anastomosantesque, apicibus liberis, 1.5 μ diametro; asci cylindrici pachydermei juventute, 60 $\times$ 8 μ; ascosporae octonae, fasciculatim dispositae, hyalinae, 18–22-loculares, protoplastis rotundatis, aciculares, subcurvatae, apicibus obtusis, 56 $\times$ 2.5 μ.

Thallus epiphloeodal, somewhat rimulose, 135 μ thick, citrine drab to deep olive, margin 3 mm. wide, of radiating, plumose strands; homoeomerous, the filaments of *Trentepohlia* more or less vertical, 6–8 μ in diameter. Pseudostromata thalline, pulvinate, irregularly rounded, 1 mm. in diameter, containing 12–20 ellipsoidal perithecia; parathecium entire, 12–15 μ thick, pseudoparenchymatous from periclinal hyphae, the upper portion dark brown shading to hyaline below; hypothecium scarcely differentiated; paraphyses dichotomous and anastomosing, 1.5 μ in diameter, tips free in the thecial gel; asci cylindric, thick-walled when young, 8-spored, about 60 $\times$ 8 μ; ascospores fascicled, hyaline, 18–22-locular, protoplasts rounded, acicular, slightly curved, ends obtuse, 56 $\times$ 2.5 μ.

TRYPETHELIUM ANOMALUM Ach., Syn. Lich. 105. 1814.

Type: Specimens cited from the West Indies and Guinea, Afzelius. Müller Argau borrowed the Guinea specimen and found it a true *Trypethelium*, reducing it to synonymy with the later *T. platystomum* Mont. Vainio, presumably studying the West Indian material, referred it to *Melanotheca Achariana* Fée. Zahlbruckner followed the Müller Argau tradition and recognized the species as a true *Trypethelium*. Acharius' choice of the specific name is unfortunate as it is not an anomalous species in either *Trypethelium* or *Melanotheca*.

Thallus epiphloeodal, olive ochre, about 100 μ thick; cortex 30 μ thick, of predominantly periclinal, interwoven hyphae in a gel; algal layer 70 μ thick, of short, more or less vertical filaments of *Trentepohlia*. Pseudostromata yellow ochre, rounded, about 2 mm. in diameter or elongate and irregular from confluence, slightly constricted at the base, with many black papillae which fall away, leaving small pits; perithecia ellipsoid, about 360 μ in diameter and 500 μ tall; parathecium 30 μ thick, carbonaceous, surrounded by brown pseudostromatic tissue and covered by thalline cortex; hypothecium about 15 μ thick, of slender, densely woven hyphae; paraphyses dichotomous and anastomosing, tips free in the thecial gel; asci fusiform, 8-spored; ascospores imbricately distichous, hyaline, fusiform, one end obtuse, the other acute, 10–14-locular, protoplasts slightly rounded, 55 $\times$ 14 μ.

T. Perrotetii Fée (Ann. Sci. Nat. 23:432. 1831) may be a synonym, as Müller Argau reports that the type from Senegal, Cap Vert, Perrotet, is old and contains no spores. *T. leucostomum* (Nyl.) Dodge has white ostioles and much larger spores (85–110 × 15–18 μ).

Sierra Leone: Njala (Kori), on bark of *Anisophyllea laurina*, F. C. Deighton M4407.

TRYPETHELIUM **leucostomum** Dodge, comb. nov.

Trypethelium platystomum f. *leucostomum* Nyl., Flora 69:178. 1886.
Trypethelium anomalum f. *leucostomum* Zahlbr., Cat. Lich. Univ. 1:487. 1922.

MELANOTHECA

MELANOTHECA Fée, Suppl. Essai Crypt. Ecorces Officin. 70. 1837.

Arthopyrenia sect. *Melanotheca* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 147. 1862.
Segestrella sect. *Melanotheca* Branth & Rostr., Bot. Tidsskr. 3:257. 1869.
Pyrenula subg. *Melanotheca* Vainio, Cat. Welwitsch Afric. Pl. 2:463. 1901.
Porothelium Eschw., Syst. Lich. 18. 1824, *non* Fr. 1818, 1821.
Porodothion Fries, Syst. Orb. Veg. 262. 1825.

Type: M. *Achariana* Fée (based on *Trypethelium anomalum* Ach., West Indian plants cited, not Afzelius' Guinea plant). *Porothelium* Eschw. and *Porodothion* Fr. were based on P. *arthonioides*, *Porina compuncta* Ach., *Trypethelium anomalum* Ach., and *T. conglobatum* Ach., all except *P. arthonioides* and part of *T. anomalum* belonging in *Trypethelium* as now understood. Since *Melanotheca* has been used in its present sense, either as a genus or subgenus since it was proposed, it should be conserved. It would be unwise to select *P. arthonioides* as the type of *Porodothion*, although it was figured by Eschweiler as the invalid *Porothelium* (renamed *Porodothion* by Fries) as all species of the present *Melanotheca* would have to be transferred to *Porodothion*.

Thallus crustose, epi- or endophloeodal; cortex often poorly developed or absent; algae *Trentepohlia*. Stroma or pseudostroma usually with several perithecia, irregularly rounded or sublinear; perithecia immersed; parathecium carbonaceous, ostiole central; paraphyses either unbranched or branched and anastomosing; asci usually 8-spored; ascospores brown to black, ellipsoidal or fusiform, 4- or more celled, with rounded protoplasts; spermatiophores simple; spermatia filiform, straight or curved.

1. Pseudostromata purple; ascospores 4-locular, 24 × 12 μ; Usambara....*M. purpurascens* Müll. Arg.
1. Pseudostromata cinnabar red to red; ascospores 4-locular, 20 × 8 μ; Kenya.....*Pyrenula Gravenreuthii* Stein
1. Pseudostromata not purple or red, usually dark-colored.....2
2. Ascospores 10-locular; pseudostromata small; Abyssinia.....*M. pusilla* (Jatta) Dodge
2. Ascospores 4-locular; pseudostromata larger 3
3. Ascospores 15 μ or less long 4
3. Ascospores more than 17 μ long 5

4. Ascospores narrowly ellipsoid, 15 × 4–5 μ; thallus fuscous olive; Mozambique..... ..... *M. obscurascens* (Vainio) Dodge
4. Ascospores broadly ellipsoid, 13–14 × 8 μ; thallus drab to hair brown; Nigeria..... ..... *M. nigeriensis* Dodge
5. Perithecia entire; ascospores 19–21 × 8–9 μ, apical cells much smaller than middle ones; top of perithecium cracking away to leave an opening about 250 μ in diameter; Sierra Leone ..... *M. porosa* Dodge
5. Perithecia dimidiate or nearly so.....6
6. Ostiole white-annulate; ascospores 17–21 × 6–7 μ; Cameroons.....*M. cameroonensis* Dodge
6. Ostiole small, not white-annulate; ascospores 17–19 × 5.5–8 μ; Angola..... ..... *M. angolensis* (Vainio) Dodge

MELANOTHECA **angolensis** (Vainio) Dodge, comb. nov.

Melanotheca Achariana var. *angolensis* Vainio, Cat. Welwitsch Afric. Pl. 2:453. 1901.

Type: Angola, Golungo Alto, near Sange, on *Entandrophragma angolensis*, Welwitsch 205.

Pseudostromata thin, ostiole small, without a white annulus; nucleus almost hemispheric or depressed conoid-subspherical; paraphyses unbranched; asci 8-spored; ascospores brown, 4-locular, protoplasts lenticular, 17–19 × 5.5–8 μ.

Welwitsch 187, from the type locality and on the same species of tree, is reported to have dimidiate perithecia and perhaps belongs in *M. cameroonensis* Dodge, but I have not seen this specimen.

The whole group of species centering about *Melanotheca Achariana* Fée needs a thorough revision based on the types of all the species and varieties proposed.

MELANOTHECA **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Ondo Province, Owena near Akure, on *Theobroma*, C. A. Thorold 170.

Thallus epiphloeodes, brunneus, 90–110 μ crassitudine; cortex 27–55 μ crassitudine, decompositus, hyphis tenuissimis, verticalibus, dense intertextis, gelifactis; stratum algarum 55–65 μ crassitudine, filamentis subverticalibus *Trentepohliae* 7–8 μ diametro. Perithecia (aut stromata cum peritheciis singulis aut binis) solitaria vel confluentia, hemispherica, nucleo conico, 0.6 mm. diametro, 0.4 mm. altitudine; parathecium (aut stroma) 125 μ crassitudine ad ostiolum centralem, ad basem 240 μ grandescens, 65 μ crassitudine sub hypothecio, carbonaceum, cortice thallino 10 μ crassitudine usque ad ostiolum tectum; ostiolum subumbilicatum; hypothecium 13–14 μ crassitudine, hyphis dense intertextis; asci cylindrici, evanescentes; ascosporae octonae, late ellipsoideae, obscure brunneae, 4-loculares, protoplastis rotundatis, subaequalibus, 13–14 × 8 μ.

Thallus epiphloeodal, drab to hair brown, 90–110 μ thick; cortex 27–55 μ thick, decomposed, of densely woven predominantly vertical, very slender, gelified hyphae. Perithecia (or stromata with one or two perithecia) solitary or aggregated into small groups, lentiform, becoming hemispheric with a conic nucleus about 0.6 mm. in diameter, 0.4 mm. tall; parathecium (or stroma) 125 μ thick at the ostiole, expanding to 240 μ thick at the base, about 65 μ thick under the hypothecium, covered by a thin layer of thalline cortex 10 μ thick all the way to the

slightly umbilicate ostiole, carbonaceous; hypothecium 13–14 μ thick, of densely woven hyphae; asci cylindric, 8-spored, soon disappearing; ascospores broadly ellipsoid, dark brown, 4-locular, protoplasts rounded, subequal, 13–14 $\times$ 8 μ.

The systematic position of this species is intermediate between *Pyrenula* and *Melanotheca*. When occurring in pairs, the perithecia appear innate in a carbonaceous stroma from the complete fusion of the parathecia and the stromatal tissue. Occasionally I have found abortive perithecia in the angles at the base when the perithecia appear solitary. Unfortunately, I have had no young material to study development. I have therefore included this species also in the key to the tropical African species of *Pyrenula*.

MELANOTHECA **porosa** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Anisophyllea laurina*, F. C. Deighton M4408.

Thallus epiphloeodes, glaber, obscure olivaceo-alutaceus; cortex 120–130 μ crassitudine, hyphis periclinalibus tenuibus dense intertextis, gelifactus, paucis cum cellulis suberosis hyalinis; stratum algarum 55 μ crassitudine, filamentis disintegratis *Trentepohliae* inter cellulos suberosos decompositos; medulla non evoluta. Pseudostromata parva, irregulariter rotundata aut frequenter confluentia, lenticularia, 0.5 mm. crassitudine, sublinearia curvataque; perithecia immersa, ostiolis ad 250 μ diametro; nucleus ca. 250 μ diametro, 300 μ altitudine, pyriformis; parathecium integrum, carbonaceum, 15 μ crassitudine; hypothecium 25 μ crassitudine, hyphis periclinalibus gelifactis; paraphyses tenues, dichotome ramosae, compactae; asci 65 $\times$ 13–14 μ; ascosporae octonae, imbricatim monostichae, hyalinae dein brunneae, late ellipsoideae, 4-loculares, protoplasti lenticulares, apicales conspicue minores, 19–21 $\times$ 8–9 μ.

Thallus epiphloeodal, smooth, deep olive buff; cortex 120–130 μ thick, of slender, interwoven, mostly periclinal hyphae in a gel, with hyaline remains of bark cells in the lower portion; algal layer 55 μ thick, of disorganized filaments of *Trentepohlia* among the remains of bark cells; medulla not differentiated but hyphae penetrating deeply into the brownish bark cells. Pseudostromata small, irregularly rounded or more frequently confluent into sublinear or curved masses, about 0.5 mm. thick, lenticular in cross-section; perithecia immersed, the overlying stroma cracking away, exposing the white top of the nucleus, thus making a pseudo-ostiole about 250μ in diameter; nucleus pyriform, about 250 μ in diameter, 300 μ tall; parathecium fusing with the stroma, entire, about 15 μ thick below the hypothecium, the bark cells below blackened to a depth of about 65 μ (the distinction visible in very thin sections); hypothecium 25 μ thick, of gelified, predominantly periclinal hyphae; paraphyses slender, dichotomous, very closely packed in the nuclear gel and then appearing simple; asci 8-spored, about 65 $\times$ 13–14 μ; ascospores imbricately monostichous, hyaline, finally brownish, broadly ellipsoidal, 4-locular, protoplasts lenticular, the apical ones conspicuously smaller, 19–21 $\times$ 8–9 μ while still smoky gray, shrinking slightly when fully brown.

At first sight, this species might be mistaken for *Bathelium porosum* (Ach.) Dodge, from the West Indies, but it lacks a papilla at any stage and has smaller ascospores. Although the spores remain hyaline until late, they become brown when fully mature.

MELANOTHECA **cameroonensis** Dodge, sp. nov.

Type: Cameroons, Tombel, on *Theobroma*, C. A. Thorold 142.

Thallus endophloeodes, obscure olivaceo-alutaceus, glaber, nigro-marginatus; pseudocortex 10 μ crassitudine, cellulis suberosis nigricantibus, decompositis, tenuibus cum hyphis dense contextis; filamenta *Trentepohliae* periclinalia, 5–6 μ diametro inter cellulas suberosas penetrantia. Pseudostromata irregularia, lateribus abruptis, 250–270 μ altitudine, nigra, ostiolis depressis, albis cum annulis, hyphis et cellulis suberosis decompositis; perithecia dimidiata, subsphaerica, 300 μ diametro, 220 μ altitudine; parathecium 40 μ crassitudine, carbonaceum; hypothecium 10 μ crassitudine, hyphis tenuibus, periclinalibus, dense intertextis; paraphyses tenuissimae, dichotome ramosae; asci cylindrici, evanescentes; ascosporae octonae, imbricatim monostichae, brunneae, 4-loculares, protoplastis rotundatis, 17–21 × 6–7 μ.

Thallus endophloeodal, deep olive buff, black-margined; pseudocortex about 10 μ thick, of disintegrated, blackened cork cells with partly decomposed, densely woven, slender hyphae; periclinal filaments of *Trentepohlia* 5–6 μ in diameter, penetrating deeply into the bark. Pseudostromata of disintegrated bark cells and hyphae, quite irregular in size and shape, black with abrupt sides, about 250–270 μ tall, ostioles slightly depressed, surrounded by white rings; perithecia dimidiate, subspherical, 300 μ in diameter, 220 μ tall, immersed in the pseudostromata; parathecium 40 μ thick, carbonaceous, finally indistinguishable from the blackened pseudostroma in old perithecia which have lost their nuclei and which usually have a thin layer of blackened bark cells at their base and so appear entire; hypothecium about 10 μ thick, of slender, densely woven, predominantly periclinal hyphae, nearly disappearing as the asci mature; paraphyses very slender, dichotomous in the nuclear gel; asci cylindric, 8-spored, wall early disappearing; ascospores imbricately monostichous, brown, ellipsoid, 4-locular, protoplasts round, apical ones only slightly smaller, 17–21 × 6–7 μ.

This species differs from *M. Achariana* Fée in having dimidiate, papillate perithecia with a white annulus and umbilicate ostiole and slightly longer and slenderer ascospores.

MELANOTHECA **obscurascens** (Vainio) Dodge, comb. nov.

Pyrenula (Melanotheca) obscurascens Vainio, Bol. Soc. Broteriana II, 6:35. 1929.
Trypethelium anomalum v. *obscurascens* Zahlbr., Cat. Lich. Univ. 10:101. 1938.
Melanotheca Achariana v. *obscurascens* Zahlbr., Cat. Lich. Univ. 10:100. 1938.

Type: Mozambique, Tungue Bay, Palma, 10° 5′ S. lat., Americo Pires de Lima.

Thallus fuscous olive; perithecia partly solitary or confluent into pseudostromata; spores fuscous, 4-locular, 15 × 4–5 μ.

The dark thallus, more solitary perithecia, and smaller ascospores, should separate this species from all other members of the M. *Achariana* group.

Melanotheca **pusilla** Dodge, comb. nov.

Trypethelium pusillum Jatta, Nuovo Giorn. Bot. Ital. 14:174. 1882.

LAURERA

Laurera Reichb., Der Deutsche Botaniker seu Repert. Herbar. 15. 1841.

Meissneria Fée, Suppl. Essai Crypt. Ecorc. Officin. 65. 1837, *non* DC.
Meristosporum Mass., Atti I. R. Ist. Veneto III, 5:327. 1860.
Thelenella sect. *Meristosporum* Vainio, Etude Lich. Brésil 2:215. 1890.
Bathelium Trev., Flora 44:21. 1861 *p. p.*; Müll. Arg., Bot. Jahrb. [Engler] 6:394. 1885.

Type: M. *varia* Fée. *Meristosporum* Mass. was based on *Trypethelium meristosporum* Mont. & v. d. Bosch. *Bathelium* Trev. was intended to be the same as *Bathelium* Ach., but included species with muriform spores, citing *Meissneria varia* Fée among others. Müller Argau treated *Bathelium* Ach. as a section of *Trypethelium* and retained *Bathelium* Trev. (citing *Meristosporum* Mass. as a synonym) for the species with hyaline, muriform spores.

Thallus crustose, epi- or endophloeodal, ecorticate, with *Trentepohlia* algae. Pseudostromata containing two or more perithecia with carbonaceous parathecia; paraphyses branched and anastomosing; asci 2–8-spored; ascospores muriform, hyaline, with more or less cubical cells. This genus is the stromatic analogue of *Polyblastiopsis* and *Clathroporina*. Although widespread in the tropics, it has hitherto been reported only from Mozambique and Socotra Island, except for *Trypethelium marginatum* Fée from Senegal, Cap Vert, formerly considered a synonym of *L. madreporiformis* (Eschw.) Riddle.

1. Ascospores under 40 μ long, 4–8-locular 2
1. Ascospores over 40 μ long, 8–20-locular 4
   2. Stromata 1.5–2 mm. in diameter; ascospores 25–38 × 10–15 μ, 6–8-locular, 2–3 locellate; perithecia dimidiate; Socotra ..... *L. velata* (Müll. Arg.) Zahlbr.
   2. Stromata less than 0.6 mm. in diameter; ascospores less than 30 μ long 3
3. Ascospores 4–6-locular, 1–3 locellate, 25 × 4–10 μ; perithecia dimidiate; Socotra ..... *L. pauperrima* (Müll. Arg.) Zahlbr.
3. Ascospores 8-locular, 1–3-locellate, 30 × 11 μ; Mozambique ..... *L. astroidella* (Vainio) Zahlbr.
   4. Ascospores 12–20-locular, 40–75 × 12–15 μ; pseudostromata dark reddish brown with 2–5 perithecia each; Senegal ..... *L. marginata* (Fée) Dodge
   4. Ascospores 10-locular; Mozambique 5
   4. Ascospores 8–10-locular, 2–4-locellate, 42–45 × 14–16 μ; pseudostromata immersed in the bark, black; Nigeria ..... *L. nigeriensis* Dodge
5. Pseudostromata dark fuscous, nude, constricted at the base, 0.8 mm. in diameter; ascospores 63 × 14 μ ..... *L. elegans* (Vainio) Zahlbr.
5. Pseudostromata substramineous to white, covered by thallus, not constricted at the base, 1 mm. in diameter with 2–5 perithecia; ascospores 50–75 × 19–22 μ ..... *L. ochroleucodes* (Vainio) Zahlbr.

Laurera **marginata** Dodge, comb. nov.

Trypethelium marginatum Fée, Ann. Sci. Nat. 23:433. 1831.

LAURERA **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Moor plantation near Ibadan, on *Theobroma*, C. A. Thorold 165.

Thallus epiphloeodes, roseo-alutaceus, 30 μ crassitudine; cortex 10 μ crassitudine, decompositus; stratum algarum 20 μ crassitudine cellulis *Trentepohliae* et suberosis disintegratis. Pseudostromata 370 μ altitudine in cortice arboris immersa, irregularia, ostiolis inconspicuis; parathecium 10–12 μ crassitudine, integrum; nucleus pyriformis, 175 μ diametro, 360 μ altitudine, ostiolo 40 μ diametro; hypothecium 16–18 μ crassitudine, hyphis tenuibus dense contextum; paraphyses tenues, dichotome ramosae; asci clavati, 110 $\times$ 28 μ, evanescentes; ascosporae octonae, irregulariter distichae, hyalinae, murales, 8–10-loculares, 2–4-locellatae, protoplastis rotundatis, ellipsoideae vel subfusiformes, 42–45 $\times$ 14–16 μ.

Thallus epiphloeodal, cinnamon buff to pinkish buff, about 30 μ thick; cortex about 10 μ thick, the outer half decomposed, the inner half with structure obscured by dark granules; algal layer not sharply differentiated, about 20 μ thick, of intermingled cells of *Trentepohlia* and disintegrating cork cells. Pseudostromata black, about 370 μ thick, immersed in the bark, protruding about 30 μ, nude, very irregular in shape and size, ostioles very inconspicuous; parathecium entire, 10–12 μ thick at the base, fused with the pseudostroma above, later the underlying bark cells blackening to a depth of 50 μ; nucleus pyriform, about 175 μ in diameter, 360 μ tall, ostiole about 40 μ in diameter; hypothecium 16–18 μ thick, of densely woven, slender hyphae; paraphyses slender, dichotomously branched; asci clavate, 8-spored, about 110 $\times$ 28 μ, wall disappearing early; ascospores irregularly distichous, hyaline, muriform, 8–10-locular, 2–4-locellate, protoplasts slightly rounded, ellipsoid to subfusiform, 42–45 $\times$ 14–16 μ.

ASTROTHELIACEAE

Thallus crustose, uniform, epi- or endophloeodal (epilithic in *Lithothelium*); cortex absent or poorly developed; algae *Trentepohlia;* perithecia pyriform with long necks, usually radially arranged, nearly free or more often immersed in a stroma or pseudostroma, the necks often confluent, opening into a common ostiolar canal, rarely remaining separate, each with its own ostiole; spermatia exobasidial.

1. Ascospores septate, 3–8-locular 2
1. Ascospores muriform 4
2. Ascospore protoplasts cylindric or neary so; saxicole ..... *Lithothelium* Müll. Arg.
2. Ascospore protoplasts rounded or lenticular; corticole 3
3. Ascospores hyaline ..... *Astrothelium* Eschew.
3. Ascospores brown ..... *Pyrenastrum* Eschew.
4. Ascospores hyaline ..... *Cryptothelium* Mass.
4. Ascospores brown ..... *Parmentaria* Fée

PYRENASTRUM

PYRENASTRUM Eschw., Syst. Lich. 16. 1824.

Type: *P. septicolare* Eschw. may be chosen as the type, since *P. plicatum* described at the same time apparently has not been recognized since.

Thallus crustose, endo- or epiphloeodal, ecorticate or with a cartilaginous

almost amorphous cortex; algae *Trentepohlia.* Perithecia innate in the bark or nearly so, usually radially arranged with long concrescent necks opening in a common ostiole; parathecium entire; paraphyses branched and anastomosing; asci 4–8-spored; ascospores ellipsoid to fusiform, brown, 4–8-locular with rounded or lentiform protoplasts.

1. Perithecia spherical, 370 μ in diameter; ascospores 16–27 × 8–14 μ; Sierra Leone..... ..... *P. pruinosum* Dodge
1. Perithecia ellipsoidal 2
   2. Ascospores 13–14 × 5–6 μ; perithecia erect, 190 μ in diameter, 240 μ tall; Sierra Leone ..... *P. erumpens* Dodge
   2. Ascospores 17–19 × 5–6 μ, perithecia recumbent, 100 μ in diameter, 180μ long; Sierra Leone ..... *P. parathelioides* Dodge

PYRENASTRUM **pruinosum** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Anisophyllea laurina*, F. C. Deighton M4409.

Thallus endophloeodes, superficie olivaceo-alutacea, 250 μ crassitudine, hyphis dense intertextis et cellulis *Trentepohliae.* Pseudostromata elongata, ca. 2 mm. latitudine, in reticulo concrescentia, thallo pallidiora et plus pruinosa, verrucis hemisphaericis ad 1 mm. diametro ostiolo circumdantibus; ectostroma carbonaceum in cortice arboris 600 μ penetrans; endostroma pallidum, perithecia continens; perithecia subsphaerica, longis cum cervicibus, circum ostiolum commune ad 375 μ diametro radiantia; parathecium 15 μ crassitudine, carbonaceum, integrum; hypothecium 25 μ crassitudine, hyphis tenuibus dense contextum; paraphyses tenues, dichotome ramosae anastomosantesque, apicibus liberis; asci cylindrici, ca. 80 × 12 μ; ascosporae octonae, ellipsoideae, brunneae, 4-loculares, protoplastis rotundatis, subaequalibus, 16–27 × 8–14 μ.

Thallus endophloeodal, surface deep olive buff to olive buff, completely disorganizing the bark cells to a depth of 250 μ, filling them with slender, densely tangled hyphae and including disorganized filaments of *Trentepohlia,* not in a definite layer. Pseudostromata elongate, about 2 mm. wide, concrescent into a network, paler than the thallus and more pruinose, with small hemispheric verrucae about the ostioles up to 1 mm. in diameter; ectostroma carbonaceous, extending about 600 μ deep into the bark; endostroma not darkened, containing the perithecia, up to 375 μ in diameter, subspherical with long necks, radially arranged about the common ostiole; parathecium entire, 15 μ thick, carbonaceous; hypothecium 25 μ thick, of slender, densely woven hyphae; paraphyses dichotomously branched and anastomosing, tips free; asci cylindric, 8-spored, about 80 × 12 μ; ascospores ellipsoidal, brown, 4-locular with rounded, nearly equal protoplasts, 16–27 × 8–14 μ.

PYRENASTRUM **erumpens** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Phyllanthus discoideus,* F. C. Deighton M4397.

Thallus epiphloeodes, alutaceus, ca. 80 μ crassitudine; cortex 25 μ crassitudine, hyphis pachydermeis, periclinalibus, gelifactus; stratum algarum 55 μ crassitudine,

cellulis cylindricis *Trentepohliae*, 8 μ diametro; medulla non evoluta. Stromata erumpentia, carbonacea, orbicularia, 2 mm. diametro vel elongata, 1.5 $\times$ 4 mm., vel irregularia, parva, duobus cum ostiolis depressis, majora cum 15–20 ostiolis; ectostroma 100 μ crassitudine ab endostromate faciliter separans; perithecia ellipsoidea, 190 μ diametro, 240 μ altitudine, cervicibus excentricis brevibus in cervice communi aperientibus, 60 μ diametro ad ostiolum, inferne latiore, 150 μ altitudine; parathecium ab endostromate carbonaceo non distinctum; hypothecium 15 μ crassitudine, hyphis tenuibus dense contextum; paraphyses parce ramosae, apicibus liberis; ascosporae octonae, imbricatim monostichae, brunneae, 4-loculares, protoplastis rotundatis, subaequalibus, 13–14 $\times$ 5–6 μ.

Thallus epiphloeodal, deep colonial buff, about 80 μ thick; cortex 25 μ thick, of densely woven, mostly periclinal hyphae, highly gelified; algal layer 55 μ thick, of disoriented, subcylindric cells of *Trentepohlia*, 8 μ in diameter; medulla not differentiated. Stromata erumpent, carbonaceous, circular, about 2 mm. in diameter, or elongate, about 1.5 $\times$ 4 mm., or quite irregular, the smaller ones with only 2 depressed ostioles, the larger with 15–20 ostioles; the ectostroma about 100 μ thick, tending to crack away from the equally carbonaceous endostroma in sectioning; perithecia ellipsoidal, about 190 μ in diameter, 240 μ tall, neck excentric, rather short, opening into the common neck of the group, about 60 μ in diameter at the ostiole, wider below, about 150 μ tall; parathecium not distinct from the endostroma; hypothecium about 15 μ thick, of slender, densely woven hyphae; paraphyses little-branched, tips free; asci 8-spored; ascospores imbricately monostichous, brown, 4-locular, protoplasts rounded, subequal, 13–14 $\times$ 5–6 μ.

PYRENASTRUM **parathelioides** Dodge, sp. nov.

Type: Nigeria, Moor plantation near Ibadan, on *Theobroma*, C. A. Thorold 169.

Thallus epiphloeodes, olivaceo-alutaceus, 65 μ crassitudine; cortex 55 μ crassitudine, gelifactus, hyphis tenuissimis periclinalibus; stratum algarum 10 μ crassitudine, cellulis *Trentepohliae* compactis; medulla non evoluta. Stromata 0.6–0.7 mm. diametro, 0.2 mm. altitudine, carbonacea, lenticularia, thallo tecta, senectute dimidia parte supera frangente ut in speciebus *Pyrenulae;* perithecia solitaria vel geminatim disposita, cervicibus brevibus in ostiolo communi aperientibus, ellipsoidea, 100 μ diametro, 180 μ longitudine; parathecium integrum, 12–15 μ crassitudine, carbonaceum; hypothecium 20 μ crassitudine, hyphis tenuibus dense contextum; asci cylindrici, 85 $\times$ 12 μ; ascosporae octonae, ellipsoideae, brunneae, 4-loculares, protoplastis rotundatis, apicalibus minoribus, 17–19 $\times$ 5–6 μ.

Thallus epiphloeodal, olive buff, about 65 μ thick; cortex 55 μ thick, gelified, of very slender periclinal hyphae; algal layer compact, 10 μ thick, of *Trentepohlia* cells, which occasionally penetrate deeply into the bark; medulla not differentiated but hyphae penetrate deeply and disorganize the bark cells. Stromata 0.6–0.7 mm. in diamater, 0.2 mm. tall, lenticular, carbonaceous, covered by the thallus which finally cracks off along with the upper half of the stroma, exposing cup-shaped depressions as seen in some species of *Pyrenula;* perithecia solitary or mostly in

pairs, necks short, emptying into a common ostiole, ellipsoidal with the long axis parallel to the substrate, up to 100 μ in diameter and 180 μ long; parathecium carbonaceous, entire, usually concrescent with the stroma, rarely cracking apart; hypothecium 20 μ thick, of densely woven, slender hyphae; asci cylindric, 8-spored, about 85 $\times$ 12 μ; ascospores ellipsoid, brown, 4-locular, protoplasts rounded, the apical ones finally much smaller than the middle ones, 17–19 $\times$ 5–6 μ.

Sections of a stroma with a solitary perithecium closely resemble those of *Parathelium* with a short, lateral neck, whence the name. Old material, after the upper portion of the stroma has cracked off, might be mistaken for an old thallus of *Pyrenula.*

Cypheliaceae

Thallus crustose, uniform or effigurate, ecorticate, with protococcoid or *Trentepohlia* algae; mazedia sessile or immersed in subcylindric thalline warts, with or without a parathecium.

1. Thallus with protococcoid algae 2
1. Thallus with *Trentepohlia* 4
   2. Ascospores unicellular 3
   2. Ascospores 2–4-locular ..... *Cyphelium* Ach.
3. Mazedia lecideine; ascospores hyaline ..... *Farriola* Norm.
3. Mazedia lecanorine; ascospores finally brown ..... *Carlosia* Samp.
   4. Asci polysporous ..... *Tylophorella* Vainio
   4. Asci 8-spored 5
5. Mazedium with only parathecium, ascospores 2–4-locular ..... *Pyrgillus* Nyl.
5. Mazedium with both parathecium and amphithecium; ascospores mostly 2-locular ..... *Tylophoron* Nyl.
5. Mazedium with both parathecium and amphithecium; ascospores 4-locular, 2-locellate ..... *Schistophoron* Stirton

TYLOPHORON

Tylophoron Nyl., Bot. Zeit. 20:279. 1862.

Type: not designated, based on *T. protrudens* Nyl. and *T. moderatum* Nyl.

Thallus crustose or disappearing; with *Trentepohlia* algae. Mazedium immersed in a subspherical thalline wart at first, then sessile, subcylindric with an open disc; both parathecium and ampithecium present; hypothecium hyaline or brownish; asci cylindric, 8-spored; ascospores 2-(rarely 3-)locular, subspherical to ellipsoid or subfusiform with a thick epispore; spermogonia immersed in the thallus with a hyaline wall; spermatiophores cylindric, slightly branched; spermatia acicular, straight.

Ascospores 8 $\times$ 4 μ; mazedia 0.6–1 mm. in diameter, 0.2–0.4 mm. tall; Mozambique ..... *T. ascidioides* Vainio
Ascospores 9–11 $\times$ 5–7 μ; mazedia 0.2–0.3 mm. in diameter; Usambara ..... *T. moderatum* v. *modestius* Zahlbr.

Tylophoron ascidioides Vainio, Bol. Soc. Broter. II, 6:173. 1929.

Type: Mozambique, Ponta Vermelha, lignicole, Pires de Lima 25.

Thallus epiphloeodal, white (slightly greenish when moist), homoeomerous, 40–50 μ thick, of disorganized filaments of *Trentepohlia*, with very slender hyaline hyphae, a few filaments of *Trentepohlia* penetrating between layers of bark cells.

Mazedium cylindric or constricted at the base, about 0.5 mm. in diameter, 0.7 mm. tall, disc urceolate at first, becoming slightly convex at maturity; amphithecium about 180 μ thick, of slender, densely woven hyphae containing large crystals, but no algal cells seen; parathecium slightly developed; hypothecium of slender vertical hyphae, slightly brownish, 250 μ tall; thecium 120 μ tall; asci cylindric to clavate, 8-spored; paraphyses slender, forming the capillitium; ascospores monostichous, brown, nearly cylindric, 2-locular, sometimes slightly constricted at the septum, wall relatively thick, 8–11 $\times$ 4 μ.

Our specimen has smaller mazedia and slightly longer spores than in the type, but we have preferred to refer it here in the absence of more specimens to show the amount of variability to be expected in the genus.

Nigeria: Ondo Province, Owena near Akure, on *Theobroma*, C. A. Thorold 168.

Cryptotheciaceae

Thallus crustose, epiphloeodal, of very loosely woven hyphae, a true cortex not developed, but the algal layer covered by a layer of hyphae, somewhat more densely woven than those of the medulla; algae *Trentepohlia;* asci 1–8-spored, borne singly throughout the thallus usually in the medulla, rarely in the algal layer, bitunicate and pushing up to the surface for spore discharge; ascospores septate to muriform.

The thallus resembles that of a sterile *Crocynia* or of *Chiodecton* subg. *Byssophorum*, and it is possible that some species referred to these genera may be found to belong in this family. In some species, the brownish tips of the resting asci may be seen at the surface under relatively high magnifications.

Santesson (Foliicolous Lichens I. Symb. Bot. Upsal. 12:1:57–68. 1952) transferred the family to the Arthoniaceae and included a group of species from *Arthonia* and *Arthothelium* in *Stirtonia* and *Cryptothecia* respectively. In this group, the asci are borne in groups in a sort of primitive (?) ardella, without clearly developed paraphyses, often showing a disc at the surface of a slightly different color (fertile areas) from that of the rest of the thallus. While we cannot be certain until we have more data of their development, it is probable that they should be segregated as different genera. For completeness I have included species of this group in the keys. Miss A. L. Smith mentions a thin, hyaline or slightly brownish peridium about each ascus, but I have found no such differentiation in the numerous specimens I have studied. Apparently, the expanding ascus pushes aside the medullary hyphae, so that they are more compact about the asci. The "paraphyses" of some descriptions are only the medullary hyphae between the asci, and are neither true paraphyses nor paraphysoids.

Ascospores bilocular, small ..... *Stirtoniopsis* Groenh.
Ascospores septate, 8–14-locular ..... *Stirtonia* A. L. Smith
Ascospores muriform ..... *Cryptothecia* Stirton

CRYPTOTHECIA

Cryptothecia Stirton, Proc. Phil. Soc. Glasgow 10:164. 1876.

Myriostigma Krmplh., Lich. Foliic. quos legit O. Beccari annis 1866–1867 in insula Borneo, 22. 1874; Nuovo Giorn. Bot. Ital. 7:44. 1875.

Myxotheca Ferd. & Winge, Bot. Tidsskr. 30:212. 1910.

Type: *C. subnidulans* Stirton. *Myriostigma* was based on M. *candidum* Krmplh. Although *Myriostigma* antedates *Cryptothecia*, Santesson has proposed the latter as a *nomen conservandum*. *Myxotheca* was based on M. *hypocreoides* Ferd. & Winge.

Thallus spreading, smooth or minutely furfuraceous, whitish to pale glaucous, margins sometimes fimbriate; cortex scarcely differentiated, intricate, slightly more compact than the medulla; algal layer of *Trentepohlia* filaments, more or less disorganized; medulla relatively thick, loosely woven, of slender hyphae; asci widely scattered throughout the medulla, rarely in the algal layer, pyriform to subspherical, thick-walled when young, 1–8-spored; ascospores hyaline, muriform, ellipsoid to subspherical.

1. Ascospores small, 20–38 × 8–14 μ, asci 4-spored 2
1. Ascospores much larger 3
   2. Thallus lacerate in long, irregular lobes, pseudo-ardella with a pale flesh-colored disc; ascospores 20–38 × 8–14 μ; foliicole; Angola ..... *Arthothelium laceratum* (Vain.) Zahlbr.
   2. Thallus continuous; asci very scattered, no disc present; ascospores 28 × 14 μ; corticole; Nigeria ..... *C. nigeriensis* Dodge
3. Asci monosporous, rarely 2-spored 4
3. Asci 8-spored 5
   4. Ascospores 50–75 × 20–32 μ; Cameroons ..... *C. subnidulans* Stirton
   4. Ascospores 40 × 35 μ; Nigeria ..... *C. Thoroldi* Dodge
5. Ascospores 20-locular, 4–5-locellate, 70–125 × 25–30 μ, sharply bent; Usambara ..... *C. geniflexum* (Müll. Arg.) Sant.
5. Ascospores 12–14-locular, 4–6-locellate, 70–95 × 25–35 μ, curved but not sharply bent; Usambara ..... *Arthothelium dictyophorum* Müll. Arg.
5. Ascospores about 10-locular, 4–6-locellate 6
   6. Ascospores 70–100 × 25–50 μ; Cameroons ..... *C. Stirtoni* A. L. Smith
   6. Ascospores 60–80 × 25–35 μ; Usambara ..... *C. caesioalba* (Müll. Arg.) Sant.

Cryptothecia nigeriensis Dodge, sp. nov.

Type: Nigeria, Ina near Ibadan, on *Theobroma*, C. A. Thorold 151a.

Thallus subarachnoideus, pallide griseus, epiphloeodes, 50–200 μ crassitudine, superficie inaequali; ecorticatus; stratum algarum 25–40 μ crassitudine, filamentis verticalibus *Trentepohliae*, cellulis 5–6 μ diametro, cylindricis vel subsphaericis; medulla hyphis tenuibus, 1 μ diametro, granulis inspersis, laxe intertextis; asci solitarii in medulla sparsi, subsphaerici, 40 μ diametro, pachydermei; ascosporae quaternae, hyalinae, ellipsoideae, murales, ca. 28 × 14 μ.

Thallus subarachnoid, light mineral gray, epiphloeodal, 50–200 μ thick, surface irregular; ecorticate; algal layer 25–40 μ, of more or less vertical filaments of *Trentepohlia* 5–6 μ in diameter, cells cylindric to subspheric; medulla of loosely woven hyphae about 1 μ in diameter, more or less inspersed with minute granules; asci borne singly in the medulla, subspherical, about 40 μ in diameter, very thick-walled, 4-spored; ascospores hyaline, ellipsoidal, muriform, about 28 × 14 μ.

CRYPTOTHECIA **Thoroldi** Dodge, sp. nov.

Type: Nigeria, Ondo Province, Owena near Akure, on *Theobroma*, C. A. Thorold 163.

Thallus epiphloeodes, 135 μ crassitudine, byssoideus, pallide griseus, margine albo, byssoideo; pseudocortex 25 μ crassitudine, hyphis erectis 2–3 μ diametro, laxe intertextis; stratum algarum 15–25 μ crassitudine, filamentis *Trentepohliae*, plus minusve periclinalibus, 4 μ diametro; medulla 85 μ crassitudine, hyphis tenuibus laxe intertextis; asci solitarii, in strato algarum sparsi, pyriformes vel subsphaerici, 43 $\times$ 27–35 μ, juventute pachydermei, monospori; ascosporae hyalinae, muriformes, 40 $\times$ 26–34 μ.

Thallus epiphloeodal, 135 μ thick, byssoid, spongy, light mineral gray with a white byssoid margin; pseudocortex 25 μ thick, of erect hyphae 2–3 μ in diameter, forming a velvety surface; algal layer 15–25 μ thick, of more or less periclinal filaments of *Trentepohlia* about 4 μ in diameter; medulla 85 μ thick, of very slender, loosely woven, hyaline hyphae; asci monosporous, borne singly in the algal layer, pyriform to subspheric, 43 $\times$ 27–35 μ, thick-walled when young; ascospores hyaline, muriform, 40 $\times$ 26–34 μ.

ARTHONIACEAE

Thallus crustose, uniform, homeo- or heteromerous, epi- or endophloeodal, ecorticate, with *Palmella*, *Trentepohlia* or *Phyllactidium* algae; ardella without parathecium, variable in shape from rounded, elongate, or radially branched, usually single (in a stroma in *Synarthonia*); paraphyses branched and anastomosing to form a thick epithecium; asci subspheric to broadly pyriform; ascospores septate or muriform.

1. Ardellae immersed in a stroma; ascospores becoming brown; algae *Trentepohlia* ..... *Synarthonia* Müll. Arg.
1. Ardellae solitary 2
   2. Algae *Trentepohlia* 3
   2. Algae *Palmella* 4
   2. Algae *Phyllactidium;* foliicole ..... *Arthonia* Ach.
3. Ascospores septate ..... *Arthothelium* Mass.
3. Ascospores muriform ..... *Allarthonia* Nyl.
   4. Ascospores septate ..... *Allarthothelium* Zahlbr.
   4. Ascospores muriform ..... *Arthoniopsis* Müll. Arg.
5. Ascospores septate, hyaline ..... *Trichophyma* Rehm
5. Ascospores muriform 6

ARTHONIA

ARTHONIA Ach., Neues Jour. f. d. Bot. 1:3:3. 1806.

Ustalia Fr., Syst. Orb. Veg. 274. 1825.

Type: not designated; eight species included in the original treatment. The foliose species are now placed in *Solorina*. Of the six remaining, all belong in *Arthonia* as now recognized. *Opegrapha radiata* Pers. may be selected as the type. *Ustalia* Fr. was based on *Graphis caribaea* Ach. For a discussion of the numerous

other possible synonyms and their types, see Santesson, Foliicolous Lichens I. Symb. Bot. Upsal. 12:1:68–75. 1952.

Thallus crustose, uniform or subeffigurate, epi- or endophloeodal, or saxicolous; ecorticate or with a pseudocortex of disintegrated bark cells; algae *Trentepohlia;* medulla often scarcely developed; ardellae rounded, elongate or star-shaped, more or less immersed in the thallus; parathecium absent or the outermost paraphyses blackened forming a pseudoparathecium; paraphyses branched and anastomosing above, forming a thick epithecium; asci subspheric, pyriform, rarely ellipsoid, thick-walled when young, especially above, 8-spored; ascospores oblong-ellipsoid to clavate when the apical cell is much larger than the others, septate, 2– pluri-locular, hyaline or brownish; spermogonia superficial, wall dark, spermatiophores subcylindric; spermatia cylindric, straight or curved. Stylospores sometimes present, terminal, ovoid to ellipsoid, unicellular or septate, hyaline or brownish.

1. Ardella white or very pale 2
1. Ardella bright red to violet 3
1. Ardella dark fuscous to black 7
   2. Disc white, more or less confluent like a minute pertusarial stroma (belongs in *Stirtonia*, fide Sant.); ascospores 8–10-locular, 50–60 × 20–22 μ; Usambara..... *A. pertusariella* Müll. Arg.
   2. Disc pale flesh-color, circular or angular (belongs in *Stirtonia*, fide Sant.); ascospores 10–locular, 38–46 × 10–16 μ; Usambara..... *A. carneoalbens* Müll. Arg.
   2. Disc densely white-pruinose, pale brown below the pruina, 0.2 mm. in diameter; ascospores 4–6-locular, 18–22 × 5.5–6 μ; Sierra Leone..... *A. subcaesia* Dodge
   2. Disc yellowish white, lobulate or angular; ascospores 6–7-locular, 17–20 × 5–5.5 μ; Angola ..... *A. loangana* Müll. Arg.
3. Disc red, ascospores 2-locular, 15–20 × 6–7 μ; Mozambique..... 4
3. Disc cinnabar to violet 5
3. Disc rufescent, subpruinose; ascospores 6-locular, 30–32 × 10 μ; Mozambique..... *A. leptographoidea* (Vainio) Zahlbr.
   4. Thallus white ..... *A. erythrocarpa* Vainio
   4. Thallus pale rose, or rose spotted on white..... *A. erythrocarpa* v. *roseopallens* Vainio
5. Ardella round, disc caesio-pruinose, margin black; Mozambique..... *A. cinnabarina* v. *orbicella* Nyl.
5. Ardella oblong, disc red-pruinose, margin black; ascospores 17–22 × 5–6 μ; Angola ..... *A. cinnabarina* v. *rimata* (Vainio) Zahlbr.
5. Ardella long and narrow, disc blackish, margin red; ascospores 16–20 × 3–5 μ; Angola ..... *A. cinnabarina* v. *reducta* (Vainio) Zahlbr.
5. Ardella asteroid-branched 6
   6. Disc pruinose, then nude and darkening; Kenya..... *A. cinnabarina* v. *elegantula* Zahlbr.
   6. Disc cinnabar purple; ascospores 20 × 8 μ; Usambara..... *A. cinnabarina* v. *speciosa* Müll. Arg.
   6. Disc fuscous, pruinose; ascospores 16–18 × 3–5 μ; Angola..... *A. cinnabarina* v. *medusaeformis* (Vainio) Zahlbr.
   6. Disc violet, ardella covering an area 4–5 mm., very dendroid-branched; ascospores 17–22 × 5–6 μ; Angola..... *A. cinnabarina* v. *dendritica* Steiner
7. Ascospores 3–4-locular 8
7. Ascospores 4–5-locular, 14–18 × 5–6 μ; ardella elliptic, 0.2 mm. wide, disc red-fuscous when moist, black when dry, not pruinose; Somaliland..... *A. somaliensis* Müll. Arg.
7. Ascospores 5-locular, 16–23 × 7.5–9 μ, fuscous; ardella dendroid-branched, branches up to 3 mm. long, disc dark violet when dry, not pruinose; Socotra..... *A. gregaria* v. *dendritica* Steiner
7. Ascospores 5–6-locular 9
7. Ascospores 7–12-locular 10
   8. Ardella round, 0.4–0.5 (–0.7) mm. in diameter; ascospores 17–20 × 6 μ, with halo, 4-locular; Sierra Leone ..... *A. modesta* Dodge
   8. Ardella round, 0.5–1 mm.; ascospores 10–12 × 4–5 μ, 4-locular; Socotra..... *A. applanata* Stzbgr.
   8. Ardella elliptic to oblong, 0.3–0.5 × 0.1–0.2 mm., or round, 0.2–0.3 mm. in diameter; ascospores 12–16 × 3–4.5 μ, mostly 3-locular; Mozambique..... *A. palmensis* (Vainio) Zahlbr.

9. Ascospores 18–20 × 4–5 μ; ardella 0.5 × 1 mm., disc black; Sierra Leone.....*A. elevata* Dodge
9. Ascospores 28 × 11–12 μ; ardella 0.5–0.8 × 0.12–0.15 mm., disc fuscous black; Angola .....*A. leptogramma* Müll. Arg.
9. Ascospores 30–32 × 10 μ; ardella 0.2–0.5 × 0.1–0.15 mm., disc rufescent; Mozambique .....*A. leptographoidea* (Vainio) Zahlbr.
10. Ascospores 22–30 × 8–9.5 μ; ardella 0.5 × 0.25 mm.; Kenya.....*A. ilicinodes* Steiner
10. Ascospores 24 × 8–9 μ; ardella 0.5–1 × 0.1–0.5 mm.; Mozambique..... .....*A. microcarpella* (Vainio) Zahlbr.
10. Ascospores 24–27 × 10.5–13.5 μ, 8-locular; ardella round, 0.5 mm. in diameter; Sierra Leone .....*A. leptogrammodes* Dodge
10. Ascospores 50–60 × 18–20 μ, 10–12-locular; ardella round, 0.5–1 mm. in diameter; Socotra .....*A. calospora* Müll. Arg.

ARTHONIA **modesta** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Peltophorum africanum* v. *speciosum*, F. C. Deighton M4342.

Thallus endophloeodes, superficie fumoso-griseus; pseudocortex ad 25 μ crassitudine, cellulis suberosis decompositis et hyphis tenuibus hyalinis; stratum algarum ad 20 μ crassitudine, filamentis periclinalibus *Trentepohliae* inter cellulas suberosas decompositas. Ardella orbicularis, modice convexa, 0.4–0.5(–0.7) mm. diametro, disco nigro; hypothecium non bene evolutum; thecium 80 μ altitudine; paraphyses tenues, superne ramosae anastomosantesque, epithecium brunneum, ca. 20 μ crassitudine super ascos formantes; asci ellipsoidei vel subpyriformes, 30 × 20 μ, apicibus incrassatis; ascosporae octonae, hyalinae, halone circumdatae, (3-)4-loculares, late clavatae, cellula apicali majore, 17–20 × 6 μ.

Thallus pale smoke gray to smoke gray; endophloeodal; pseudocortex up to 25 μ thick, of disintegrated bark cells and very slender, hyaline hyphae; algal layer up to 20 μ thick, of periclinal filaments of *Trentepohlia* in and between disintegrated bark cells, with a few medullary hyphae penetrating more deeply into the bark. Ardella circular, 0.4–0.5(–0.7) mm. in diameter, moderately convex, disc black; hypothecium not differentiated, the asci and paraphyses appearing to arise from disintegrated bark cells; thecium 80 μ tall in the center, slightly lower toward the margin; paraphyses, slender, branched and anastomosing above the asci, forming a brownish epithecium about 20 μ thick; asci ellipsoid to subpyriform, 8-spored, about 30 × 20 μ, tip thickened, protoplast broadly mamillate; ascospores hyaline, broadly clavate, with a thin halo, 3–4-locular, terminal cell somewhat larger, 17–20 × 6 μ.

ARTHONIA **elevata** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Anisophyllea laurina*, F. C. Deighton M4406.

Thallus endophloeodes, albidus, pruinosus; pseudocortex 25 μ crassitudine, cellulis suberosis decompositis et hyphis hyalinis tenuissimis; stratum algarum 50 μ crassitudine, filamentis verticalibus *Trentepohliae* et cellulis suberosis decompositis. Ardella ad 1 mm. diametro, orbicularis vel oblonga (dein 0.5 × 1 mm.), disco nigro, pseudolecideina; pseudoparathecium paraphysibus nigricantibus; thecium 65 μ altitudine; hypothecium 10 μ crassitudine hyphis periclinalibus pallide brunneis; asci pyriformes vel subsphaerici, pachydermei, 32 × 25 μ; ascosporae

octonae, fasciculatim dispositae, clavatae, hyalinae, 5–6-loculares, 18–20 × 5–6 μ.

Thallus endophloeodal, nearly white, pruinose, subrimose on very rimose bark; pseudocortex about 25 μ thick, of disintegrated bark cells and very slender hyphae; algal layer about 50 μ thick, of short, vertical, partly disorganized filaments of *Trentepohlia* and some disintegrated bark cells; medulla not differentiated but medullar hyphae penetrating some distance into the bark and disorganizing the cells. Ardella round, up to 1 mm. in diameter or oblong, then about 0.5 × 1 mm., disc black, convex, seated on bark cells less disintegrated than in the surrounding thallus, thus appearing elevated and lecideoid (rarely lecanoroid); pseudoparathecium of blackened paraphyses, progressively paler within; thecium 65 μ tall in the center, somewhat lower toward the margin with younger asci; hypothecium 10 μ thick, of pale brownish periclinal hyphae; asci pyriform to subspheric, 8-spored, 32 × 25 μ when nearly mature, thick-walled; ascospores fascicled, clavate, hyaline, 5–6-locular, 18–20 × 5–6 μ.

ARTHONIA **leptogrammodes** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Lagerstroemia speciosa*, F. C. Deighton M4347.

Thallus epiphloeodes, albidus, tenuissimus, tenuissime nigromarginatus; ecorticatus; filamentis *Trentepohliae*, 5–6 μ diametro, hyphisque tenuissimis, crystallis minutis nubilatis. Ardella orbicularis, 0.5 mm. diametro, rare 2–3-confluentia, disco nigro, immarginata; hypothecium hyalinum, tenue; thecium 55 μ altitudine; paraphyses tenues, ramosae anastomosantesque, superne brunneae; asci pyriformes, 35 × 25 μ, juventute pachydermei protoplastis mamillatis, dein leptodermei; ascosporae octonae, hyalinae, polystichae, halone tenui circumdatae, ad 8-loculares, cellula apicali 9 μ longitudine, basali 6 μ, intermedii 2 μ longitudine, 24–27 × 10.5–13.5 μ.

Thallus epiphoeodal, white, very thin, with a narrow black margin; algae *Trentepohlia*, filaments 5–6 μ in diameter, partly disorganized and surrounded by very slender hyphae covered with minute crystals. Ardella nearly circular, 0.5 mm. in diameter, rarely 2–3 confluent, disc black, immarginate; hypothecium very thin and hyaline; thecium 55 μ tall; paraphyses slender, branched and anastomosing, slightly brownish above; asci pyriform, 8-spored, thick-walled when young, especially above, protoplast mamillate, becoming quite thin-walled at maturity; ascospores hyaline (a few slightly smoky as if finally becoming brown) with a thin halo, up to 8-locular, the apical cell 9 μ, the basal cell 6 μ, the intermediate cells about 2 μ long, 24–27 × 10.5–13.5 μ.

Perhaps closest to *A. leptogramma* Müll. Arg. in size and shape of the ascospores, although both terminal cells are much larger than the middle cells, which is very unusual in the whole genus *Arthonia*. The ardella is completely different in size and shape.

ARTHONIA (PACHNOLEPIA) **subcaesia** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Bauhinia tomentosa*, F. C. Deighton M4307H.

Thallus epiphloeodes, tenuissimus, albidus, tenuiter nigro-marginatus, cellulis cylindricis *Trentepohliae* et hyphis tenuissimis, superne crystallis minutis nubilatis. Ardella orbicularis vel suboblonga, erumpens, disco dense caesio-pruinoso, 0.2 mm. diametro; hypothecium 50 μ crassitudine, pallide brunneum, hyphis tenuibus cum crystallis; thecium 50 μ altitudine; paraphyses tenues, ramosae anastomosantesque; asci pyriformes, 35–40 $\times$ 18–20 μ, juventute pachydermei; ascosporae octonae, polystichae, clavatae, hyalinae, 4–6-loculares, 18–22 $\times$ 5.5–6 μ.

Thallus epiphloeodal, very thin, white to pearl gray with a narrow black margin, nearly homoeomerous; algal cells of *Trentepohlia*, cylindric, from disorganized filaments, surrounded by very slender, tangled hyphae, the outer portions covered by minute crystals. Ardella round to slightly oblong, erumpent, disc densely white-pruinose (pale brownish when the pruina is rubbed off), about 0.2 mm. in diameter; parathecium not differentiated; hypothecium about 50 μ thick, pale brownish, of slender hyphae covered with crystals; thecium 50 μ tall; paraphyses slender, branched and anastomosing to form the epithecium above the asci; asci 8-spored, pyriform, 35–40 $\times$ 18–20 μ, very thick-walled, especially above, when young; ascospores polystichous, clavate, hyaline, 4–6-locular, 18–22 $\times$ 5.5–6 μ.

OPEGRAPHACEAE

Thallus crustose, cortex poorly developed or absent, algae *Palmella* (Xylographeae), *Trentepohlia* (Opegrapheae), or *Phyllactidium* (Micrographeae); medulla poorly developed or absent. Lirellae simple or branched, usually sessile, rarely immersed, single (with two parallel thecia per lirella in *Ptychographa* and *Diplogramma*); parathecium usually thick, black, and carbonaceous (rudimentary in *Gymnographa*); ascus more or less clavate with 8 or less ascospores; ascospores unicellular, septate, or muriform, walls and septa thin, protoplasts cylindric in septate spores, appearing cubical in muriform spores.

1. Algae *Palmella* (Xylographeae) 2
1. Algae *Trentepohlia*, ascospores septate or muriform (Opegrapheae) 6
1. Algae *Phyllactidium* (Micrographeae) 9
2. Ascospores unicellular 3
2. Ascospores septate ..... *Aulaxina* Fée
2. Ascospores muriform 4
3. Lirellae with a single thecium each ..... *Ptychographa* Nyl.
3. Lirellae with two parallel thecia each ..... *Xylographa* Fr.
4. Hypothecium pale; on wood, rarely on bark ..... *Lithographa* Nyl.
4. Hypothecium dark; saxicolous ..... *Encephalographa* Mass.
5. Ascospores bilocular, lirellae caespitose ..... *Diplogramma* Müll. Arg.
5. Ascospores 4-locular, 2 parallel thecia per lirella 7
6. Ascospores hyaline 8
6. Ascospores finally brown ..... *Opegrapha* Pers.
7. Ascospores septate ..... *Helminthocarpon* Fée
7. Ascospores muriform ..... *Gymnographa* Müll. Arg.
8. Lirellae immersed; parathecium rudimentary ..... *Sclerographis* Zahlbr.
8. Lirellae sessile; parathecium well developed ..... *Fouragea* Trev.
9. Ascospores hyaline ..... *Micrographa* Müll. Arg.
9. Ascospores brown .....

OPEGRAPHA

Opegrapha Pers., Neue Ann. Bot. [Usteri] 1:23, 29–32. 1794, *non* Humb., Fl. Friberg. Specim. 57. 1793.

Alyxoria S. Gray, Nat. Arr. Brit. Pl. 1:101. 1821.
Hysterina S. Gray, Nat. Arr. Brit. Pl. 1:504. 1821.
Scaphis Eschw., Syst. Lich. 14. 1824.
Oxystoma Eschw., Syst. Lich. 14. 1824.
Zwackhia Koerb., Syst. Lich. Germ. 284. 1854.
Xylastra Mass., Framm. Lich. 10. 1855.

Type: *Opegrapha* Humb. was based on *Lichen scriptus* L. and its varieties, which species has been the type of *Graphis* since that genus was founded. However, *Opegrapha* Pers. 1794 has been universally recognized in the present sense since its publication and being based wholly on species now included in the genus, it should be conserved against *Opegrapha* Humb. 1793; otherwise all the species now in *Graphis* would have to be transferred to *Opegrapha* and all those now in *Opegrapha* would have to be transferred to *Alyxoria* or *Hysterina*. In his generic description, Persoon cites *Lichen scriptus* var. a. *L. rugosus* L., Hoffm., which later in the discussion of the species he cites as a synonym of his *O. faginea*. This entity is now considered a fungus; hence in selecting a type from the other 13 species, it would be better to select another species, such as *O. lichenoides* Pers. to conserve the genus in its present sense.

Alyxoria Ach. in S. Gray was based on *Opegrapha notha* Ach. and *O. diaphora* Ach. *Hysterina* S. Gray was based on 12 species still included in *Opegrapha*. *Scaphis* Eschw. was based on *O. notha* Ach. (figured) and on *S. anfractuosa* Eschw. and *S. compressa* Eschw. *Oxystoma* Eschw. was based on *O. cylindrica* Raddi. *Zwackhia* Koerb. was based on *Z. involuta* (Wallr.) Koerb. *Xylastra* Mass. was based on *Arthonia fuscescens* Fée.

Thallus crustose, uniform, ecorticate or nearly so, either saxicole or corticole; algae *Trentepohlia;* lirellae immersed to sessile, lips somewhat connivent, nearly closed to open, especially when wet; parathecium entire or dimidiate (in sect. *Pleurothecium*); paraphyses branched and anastomosing above the asci; asci clavate, 8-spored; ascospores ellipsoid to fusiform, straight or slightly curved, hyaline, septate, 2–18-locular, protoplasts cylindric; spermatia exobasidial, filiform, straight or curved. Stylospores sometimes present, terminal, ovoid to long-ellipsoid, straight or slightly curved, hyaline.

In the following key, the species are corticole unless otherwise stated:

1. Perithecium entire (Euopegrapha) 2
1. Perithecium dimidiate (Pleurothecium) 14
   2. Ascospores 4-locular 3
   2. Ascospores 4–9-locular 8
   2. Ascospores 10–14-locular 13
3. Thallus and disc ochraceo-pruinose; lirellae 0.3–2 × 0.25–0.3 mm., simple or rarely forked; ascospores 14 × 4 μ, without halo; Angola ..... *O. Vainioi* Zahlbr.
3. Thallus and disc not pruinose 4

4. Ascospores more than 18 μ long; thallus white 5
4. Ascospores less than 18 μ long 6
5. Lirellae sessile, 0.3–0.5 × 0.2 mm.; ascospores 35–40 μ long; São Thomé.....*O. subnothella* Nyl.
5. Lirellae semi-immersed, 0.2–0.8 × 0.2–0.3 mm.; ascospores 18–23 × 3–4 μ; Angola .....*O. albocinerea* Vainio
6. Thallus white 7
6. Thallus yellowish green; ascospores 13–15 × 4–5 μ, with halo; lirellae 1.5–1.7 × 0.2–0.8 mm.; Boroma on Zambesi River.....*O. Menyhartii* Müll. Arg.
6. Thallus pale clay color, subfarinose; ascospores 16 × 6 μ; lirellae 1.5–2.5 × 0.5 mm.; Socotra .....*O. sororiella* Müll. Arg.
7. Thallus chalky white; saxicole; ascospores 16–18 × 4 μ; Senegal.....*O. alboatra* Nyl.
7. Thallus whitish-granulate; corticole; ascospores 14–15 × 4.5 μ; São Thomé.....*O. lepidella* Nyl.
7. Thallus white, thin; corticole; ascospores 13–15 × 3–3.5 μ; Ascension Island..... .....*O. aterula* Müll. Arg.
8. Ascospores more than 27 μ long; thallus ashy to glaucescent.....9
8. Ascospores less than 27 μ long 10
9. Ascospores 26–30 × 6–6.5 μ, 6–8-locular, cells subequal, no halo; thallus ashy; lirellae 0.2–0.5 × 0.1 mm.; Kenya.....*O. viridulata* Steiner
9. Ascospores 30–34 × 4–5 μ, 8–10-locular, cells subequal; lirellae angular or reniform; calcicole; Socotra .....*O. cretacea* Müll. Arg.
9. Ascospores 32–45 × 5–6 μ, with halo, 6–8-locular, one or two middle cells much longer than the others; thallus pale glaucescent; lirellae 0.3–1 × 0.15–0.25 mm.; Angola .....*O. septemseptata* Vainio
9. Ascospores 27.5–40 × 4–5 μ, without halo, 7–9-locular; thallus ashy to glaucescent; lirellae 0.2–0.7 × 0.1 mm.; Mozambique.....*O. delicata* Vainio
10. Thallus pale or ashy 11
10. Thallus pale yellowish or glaucous 12
10. Thallus fusco-virescent; ascospores 16–21 × 5–6 μ, 4–8-locular; lirellae straight; Ilha Principe .....*O. leptographa* Nyl.
11. Ascospores 20 × 4.5 μ, 6-locular; thallus ashy; lirellae rounded, 0.4–0.5 mm. in diameter, or elongate, 0.8–1.5 × 0.4–0.5 mm.; base of parathecium thinner than the sides; Usambara .....*O. rufa* Müll. Arg.
11. Ascospores 20–25 × 4–5 μ, 8–9-locular; thallus pale; lirellae (0.5)–3 × 0.3–0.5 mm., straight or flexuous; Mozambique.....*O. vermelhana* Vainio
11. Ascospores 15–19 × 4–5 μ, 6-locular; thallus white; Angola.....*O. loandensis* Vainio
11. Ascospores 15 × 4 μ, 4–5-locular; thallus white; lirellae long, 0.2 mm. wide, flexuous; Socotra .....*O. Dracaenarum* Müll. Arg.
11. Ascospores 20–28 × 6–7 μ, 8-locular; lirellae simple or with lateral branch, 1–1.5 mm. long; lignicole; Socotra.....*O. vestita* Müll. Arg.
11. Ascospores 18–27 × 4 μ, 8–9-locular; lirellae simple or branched, 1–1.5 × 0.2–0.25 mm.; lignicole; Socotra .....*O. elegans* Müll. Arg.
11. Ascospores 20–25 × 5 μ, 4–6-locular; lirellae immersed, simple or branched, 0.5 mm. broad; calcicole; Socotra .....*O. subcalcarea* Müll. Arg.
12. Ascospores 19–21 × 3–4 μ, 4–6-locular; thallus pale yellowish-glaucous; lirellae radially branched, immersed; Nigeria.....*O. nigeriensis* Dodge
12. Ascospores 11–13 (–15) × 3–3.5 μ, 4–6-locular; thallus pale yellow, rimulose, finally cracking away; lirella 2 × 0.25 mm.; Socotra.....*O. microspora* Müll. Arg.
13. Ascospores 47–57 × 7–9 μ, 12–14-locular; lirellae simple, 1–2.2 mm. long; Sierra Leone .....*O. prosodea* Ach.
13. Ascospores 30–46 × 5–8 μ, 8–10-locular; lirellae 2–3 × 0.2 mm.; Angola....*O. graphidiza* Nyl.
14. Ascospores 6-locular 15
14. Ascospores 8–14-locular 16
15. Ascospores 15–19 × 4–5 μ, apical cells larger; lirellae 1–3 × 0.3–0.4 mm.; thallus white; Angola .....*O. loandensis* Nyl. sec. Vainio
15. Ascospores 22 × 6–7 μ, apical cells larger; lirellae 1–1.5 × 0.2–0.3 mm.; simple or 2–3-forked; thallus pale greenish; Sierra Leone.....*O. humilis* Müll. Arg.
15. Ascospores 23–35 × 3.5 μ; lirellae radiately branched; thallus white; Mozambique .....*O. medusulina* Nyl.
16. Thallus olive to glaucous; ascospores 30–56 × 6–8 μ, with halo, 9–14-locular; lirellae 0.3–1 × 0.2 mm., simple, straight or curved; Angola.....*O. prosodeoides* Vainio

16. Thallus white or pale glaucous 17
17. Lirellae radially branched, 5 × 0.2–0.3 mm.; ascospores 9-locular, 32 × 3 μ; Mozambique ..... *O. mozambica* Vainio
17. Lirellae simple or forked 18
18. Ascospores 32–37 × 3–4 μ, 8–9-locular; lirellae white, 0.3–2.5 × 0.2–0.4 mm., K—; Mozambique ..... *O. frustulosa* Vainio
18. Ascospores 30–46 × 5–8 μ, 8–10-locular; lirellae 2–3 × 0.2 mm., straight or flexuous; Angola ..... *O. graphidiza* Nyl.
18. Ascospores 27–40 × 5–6 μ, 9–12-locular; lirellae 1–4 × 0.25 mm., simple or forked; thallus pale glaucous to white, K orange; Tanganyika..... *O. subgraphidiza* Zahlbr.

Opegrapha **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Ondo Province, Owena near Akure, on *Theobroma*, C. A. Thorold 164.

Thallus pallide flavo-glaucus, subpruinosus, margine albo-byssino, angusto, 240 μ crassitudine; cortex vix evolutus; stratum algarum 50 μ crassitudine, cellulis cylindricis *Trentepohliae* isodiametricis; medulla 190 μ crassitudine, duobus stratis sistens, superum 135 μ crassitudine hyphis tenuibus hyalinis laxe intertextis, inferum 55 μ crassitudine hyphis periclinalibus dense contextum. Lirellae radiato-ramosae, ad 1.5 mm. diametro, thallo immersae vel usque ad 30 μ super thallum emergentes; parathecium integrum, 80 μ altitudine, carbonaceum, labiis conniventibus; hypothecium vix evolutum; thecium rotundatum, 40 μ altitudine; paraphyses tenues, ramosae anastomosantesque, epithecium obscure brunneum 8–10 μ crassitudine formantes; asci ellipsoidei, 24 × 8 μ, leptodermei; ascosporae octonae, hyalinae, 4–6-loculares, cellulis cylindricis, 19–21 × 3–4 μ.

Thallus pale yellowish-glaucous, subpruinose, with a very narrow white byssine margin, about 240 μ thick; cortex scarcely differentiated, consisting of very slender hyphae with minute crystals extending a few micra above the algal cells; algal layer about 50 μ thick, of *Trentepohlia* cells closely packed, cylindric, nearly isodiametric, with scattered cells deeper in the medulla; medulla 190 μ thick, in two layers, the upper about 135 μ thick, of slender, hyaline hyphae, very loosely woven, the lower about 55 μ thick, of compactly woven periclinal hyphae, slightly brownish next the substratum. Lirellae radiately branched groups about 1.5 mm. in diameter, immersed in the thallus or protruding about 30 μ above the surface of the thallus; parathecium entire, 80 μ tall, 40 μ thick, carbonaceous, lips connivent; hypothecium scarcely differentiated; thecium 40 μ tall, rounded; paraphyses slender, branched and anastomosing, forming a dark brown epithecium 8–10 μ thick; asci 8-spored, ellipsoid, about 24 × 8 μ, wall thin, only slightly thickened at the tip when young; ascospores hyaline, 4–6-locular, wall rather thick but protoplasts cylindric, 19–21 × 3–4 μ.

The texture and the color of the thallus resemble those of *Chiodecton* at first sight, while the radially branched lirellae suggest a *Phaeographis*. The lirellae are distinct, without thickened and coalescent bases as in the Chiodectonaceae. They are immersed in the algal layer and the upper part of the loose medulla, not reaching the substrate as in the Graphidaceae and most other Opegraphaceae.

OPEGRAPHA PROSODEA Ach., Meth. Lich. 22. 1803.

Type: Sierra Leone, corticole, Afzelius.

Thallus epiphloeodal, between grape green and vetiver green, minutely verrucose and somewhat rimulose, without a black margin, 35–55 μ thick, almost homoeomerous; algae short vertical filaments of *Trentepohlia,* cells short-cylindric, 5–6 μ in diameter, terminal cells subspheric and slightly larger. Lirellae black, elevated, linear, straight, about 135 μ wide and up to 1.5 mm long, covered by a thin hyaline layer 5–6 μ thick, of decomposed hyphae; parathecium 25–30 μ thick below and on the vertical sides, thinning to 12–15 μ at the somewhat connivent lips, carbonaceous; hypothecium 12–15 μ thick, of slender, deeply staining hyphae; paraphyses slender, somewhat branched, tips clavate, covered by minute brownish crystals, gelifying as the asci mature; asci 8-spored, narrowly ellipsoid, 80 $\times$ 20 μ, thick-walled at first, then thin-walled except at the somewhat thickened tip; ascospores hyaline to slightly brownish when moribund, long-fusiform, 40 $\times$ 5–6 μ, 12–14-locular, walls and septa rather thick, but protoplasts cylindric.

If Nylander (Ann. Sci. Nat. Bot. IV, 11:229. 1859) was reporting the spores of the type ("ex hb."), our spores are somewhat smaller. In other respects our specimens agree well with the Acharian description, although it lacks any fuscous shade in the thallus. O. *graphidiza* Nyl. from Angola differs in a less well-developed thallus and perhaps dimidiate lirellae. Nylander states, "hypothecium fuscescens" in the formal description, using hypothecium in the sense of base of lirella, as he often did, thus implying that the parathecium is entire. He compares it, however, with the dimidiate *Graphis scripta* in the notes at the end of his description, implying that it is dimidiate. Vainio, who presumably studied the type, places it in the section *Pleurothecium* with dimidiate lirellae.

Nigeria: Ina near Ibadan, on *Theobroma,* C. A. Thorold 150.

GRAPHIDACEAE

Thallus crustose, cortex amorphous or absent, epi- or endophloeodal, with *Trentepohlia* algae (*Palmella* in *Xyloschistes*); lirellae usually more or less immersed in the thallus, or, if sessile, the sides covered with thallus until late, roundish, oblong, simple or branched, single; parathecium entire or dimidiate, carbonaceous, colored or hyaline (very rudimentary to practically absent in *Graphina* sect. *Platygrammodes*); paraphyses slender, unbranched, tips thickened and warted in *Acanthographis;* asci clavate when young becoming oblong to cylindric when mature with 8 or fewer ascospores; hypothecium hyaline or pale; ascospores hyaline or brown, septate or muriform, protoplasts rounded to lenticular.

1. Ascospores septate 2
1. Ascospores muriform 5
2. Ascospores hyaline 3
2. Ascospores brown at maturity 4
3. Paraphyses without warted and conspicuously thickened clavate tips..... *Graphis* Ach.
3. Paraphyses with conspicuously clavate and warted tips..... *Acanthographis* Wats.
4. Protoplasts of ascospores cylindric; ascospores mostly 2-locular..... *Melaspilea* Nyl.
4. Protoplasts of ascospores rounded; ascospores 4- or more locular..... *Phaeographis* Müll. Arg.

5. Ascospores hyaline 6
5. Ascospores brown 7
6. Paraphyses without thickened and warted tips ..... *Graphina* Müll. Arg.
6. Paraphyses with conspicuously clavate and warted tips ..... *Acanthotheciopsis* Zahlbr.
7. Algae *Palmella;* lignicole ..... *Xyloschistes* Vainio
7. Algae *Trentepohlia* ..... *Phaeographina* Müll. Arg.

GRAPHIS

Graphis Adans., Fam. Pl. 2:11. 1763 [uninomial nomenclature]; Ach., K. Vetensk. Akad. Nya Handl. 145. 1809.

Fissurina Fée, Essai Crypt. Ecorces Officin. 59. 1824.
Aulacographa Leight., Ann. Mag. Nat. Hist. II, 13:389. 1854.
Dyplolabia Mass., Neagenea Lich. 6. 1854.
Diplographis Mass., Atti I. R. Inst. Veneto III, 5:273. 1860.
? *Limboria* Trev., Conspect. Verruc. 15. 1860, *non* Ach.
Anomorpha Nyl., Lich. Ins. Guineens. 50. 1889.
Digraphis Clements, Gen. Fung. 59. 1909.

Type: *Lichen scriptus* L. *G. pulverulenta, G. Cerasi, G. betuligna,* and *G. serpentina* were described as new at the same time, all now often considered varieties of *G. scripta* (L.) Ach. *Fissurina* Fée was based on *F. Dumastii* Fée, now placed in *Graphis,* and *F. incrustans* Fée, now in *Graphina* Müll. Arg. *Aulacographa* Leight. was based on *Graphis elegans* Ach. *Dyplolabia* Mass. was based on *Graphis Afzelii* Ach. *Diplographis* Mass. was based on *G. rufula* Ach., now in *Graphis,* and *G. chlorocarpa* Fée, now in *Graphina. Limboria* Trev. *non* Ach. belongs here according to the description, although the species cited all belong elsewhere, i.e. *L. constellata* (Ach.) Trev. is now placed in *Diploschistes* and *L. tridens* (Eschw.) Trev. in *Phaeographis. Anomorpha* Nyl. and *Digraphis* Clements were both based on *A. turbulenta* Nyl., now usually placed in *Graphis.*

Thallus crustose, epi- or endophloeodal; ecorticate or with cortex of periclinal hyphae; algae *Trentepohlia.* Lirellae immersed to sessile, elongate or branched, very rarely short and rounded, lips nearly closed (connivent) to open, entire or sulcate; parathecium entire or dimidiate, carbonaceous or subhyaline; hypothecium thin, hyaline; paraphyses slender, unbranched, not thicker at the tips; asci clavate to subcylindric, septate, 2–many-locular, protoplasts lenticulate to subspherical; spermatia exobasidial, cylindric, relatively long (rarely observed).

1. Lirellae wholly densely white-pruinose 2
1. Lirellae not densely white-pruinose, disc sometimes slightly pruinose 4
2. Thallus rose color or partly paler; lirellae 0.2–7 mm. long, immersed; ascospores not seen, hence genus uncertain; Angola ..... *G. roseotincta* Vainio
2. Thallus scarcely visible except at bases of lirellae; São Thomé 3
2. Thallus powdery, bluish white; lirellae long, subflexuous, dimidiate; ascospores 35 × 9–10 μ (as in *G. scripta*); Kenya ..... *G. caesia* Müll. Arg.
2. Thallus yellowish; lirellae 2–3 (–4) × 1 mm., emersed; ascospores 16 × 8 μ, 4-locular; Guinea ..... *G. Afzelii* Ach.
2. Thallus pale yellow; lirellae immersed, disc open; ascospores 14–17 × 6 μ; São Thomé ..... *G. lynceodes* Nyl.
3. Ascospores 30–36 × 13–15 μ, 4-locular; lirellae 1 mm. or less long ..... *G. timidula* Nyl.
3. Ascospores 40–70 × 11–18 μ; lirellae 1–3 × 0.5 mm., lips sulcate ..... *G. albonotata* Nyl.

4. Parathecium hyaline or pale 5
4. Parathecium black, entire 6
4. Parathecium black, dimidiate 14
4. Parathecial structure unknown; ascospores 24–27 × 6–7 μ, 8-locular; thallus white; Mozambique ....*G. infida* Nyl.
5. Ascospores 12–13 × 6 μ, 4-locular; lirellae 0.5–1.3 mm. long; Usambara ....*G. hyalinella* Müll. Arg.
5. Ascospores 16 × 8 μ, 4-locular; lirellae up to 2 × 0.5 mm.; Nigeria ....*G. nigeriensis* Dodge
5. Ascospores 20 × 5 μ, 8-locular, with halo; thallus pale glaucous to white; lirellae immersed, 0.4–2.5 × 0.15–0.5 mm., ellipsoid; Mozambique ....*G. pallescens* Vainio
6. Ascospores 4-locular 7
6. Ascospores 8–10-locular; thallus white to glaucous 8
6. Ascospores 12–18-locular 12
7. Parathecium subimmersed, thin; ascospores 17–18 × 5–7.8 μ; Mozambique ....*G. myriocarpoides* Vainio
7. Parathecium emersed, thick on sides, very thin at base; ascospores 14–17 × 6–8 μ; Mozambique ....*G. triticella* Vainio
7. Parathecium emersed, thin but not thinner at base; ascospores 14–15 × 5–6 μ; Nigeria ....*G. Thoroldi* Dodge
8. Lirellae immersed or subimmersed 9
8. Lirellae semi- to completely emersed and sessile 10
9. Lirellae unbranched, flexuous; ascospores 23–40 × 7–9 μ, 8–10-locular; Ilha Principe ....*G. exalbata* Nyl.
9. Lirellae dichotomous, flexuous, 0.5–5 × 0.15–0.2 mm.; ascospores 20–22 × 6 μ, 8-locular; Mozambique ....*G. mocimbensis* Vainio
9. Lirellae radially branched, (0.7–) 2–4 × 0.1 mm.; ascospores 27.5–32 × 6–7.5 μ, 8–10-locular; Mozambique ....*G. myriocarpiza* Vainio
10. Lips open at maturity, disc pruinose; lirellae mostly unbranched, some forked; ascospores 50–56 × 10–12 μ, 8-locular; French Tropical Africa....*G. aperiens* v. *pruinosa* Hue
10. Lips connivent; thallus whitish 11
11. Ascospores 37–49 × 6–9 μ, 8–12-locular; lirellae short, unbranched; Guinea ....*G. comma* (Ach.) Sprgl.
11. Ascospores 25–35 × 6–7.5 μ, 8–10-locular; lirellae flexuous, unbranched or rarely forked, 0.6–0.8 × 0.1–0.15 mm.; thallus K—; Mozambique ....*G. subintricans* Vainio
11. Ascospores 24–26 × 7 μ, 8-locular; lirellae flexuous, branched, 0.7–2.5 × 0.15–0.2 mm.; thallus K yellow then red; Angola ....*G. Dracaenae* Vainio
12. Ascospores 32–45 × 7.5–8.5 μ; parathecium very thin at the base; lirellae emersed, 4–6 × 0.3 mm.; Kenya ....*G. oxyclada* Müll. Arg.
12. Ascospores 74–80 × 12–14 μ 13
12. Ascospores 90–135 × 12–17 μ; asci only 2–4-spored; lirellae emersed, 1–3 × 0.3 mm.; Usambara ....*G. superans* Müll. Arg.
13. Lirellae 2.5 mm. long, covered by thallus, lips entire; Usambara ....*G. Schroederi* Zahlbr.
13. Lirellae 4 mm. long, emersed, lips sulcate; Nigeria ....*G. ondensis* Dodge
14. Ascospores 4(-5)-locular; Mozambique 15
14. Ascospores 8–14-locular 17
15. Ascospore protoplasts connected by plasmodesmata (as in the Blasteniaceae); ascospores 18–20 × 7–8 μ ....*G. palmensis* Vainio
15. Ascospore protoplasts not connected 16
16. Ascospores 14–17 × 6–8 μ ....*G. triticella* Vainio
16. Ascospores 17.5–20 × 6–7 μ ....*G. Limae* Vainio
17. Lips striate-sulcate 18
17. Lips entire, not striate-sulcate 19
18. Ascospores 22–24 × 7 μ, without halo; Mozambique ....*G. increbrior* Vainio
18. Ascospores 32–42 × 8–9 μ, 8–12-locular; Guinea ....*G. striatula* (Ach.) Sprgl.
18. Ascospores 40–54 × 9–11 μ, 11–14-locular; lirellae long, curved, cuspidate on one side; Usambara ....*G. striatula* v. *cuspidata* Müll. Arg.
19. Lips connivent 20
19. Lips open, at least when moist 22
20. Thallus ochraceous; ascospores 25–38 × 7–8 μ, 10–14-locular; Angola ....*G. ochroplaca* Müll. Arg.
20. Thallus white to pale glaucous 21
21. Lirellae 0.3–0.7(–1) × 0.3–0.5 mm., straight, unbranched; ascospores 20–27 × 7–8.5 μ, 9-locular; Socotra ....*G. brachycarpa* Müll. Arg.

21. Lirellae 0.5(–1.8) × 0.25 mm., straight, unbranched; ascospores 30 × 8 μ, 8–10-locular; Sierra Leone ..... *G. Deightoni* Dodge
21. Lirellae very long and slender; ascospores 21–30 × 7–8 μ, 8–10-locular; Guinea.... *G. tenella* Ach.
21. Lirellae 4–6 × 0.3 mm., with 1–2 branches; ascospores 32–45 × 7.5–8 μ, 12-locular; Kenya ..... *G. oxyclada* Müll. Arg.
21. Lirellae 2 × 0.13 mm., curved, somewhat branched; ascospores 27 × 7–8 μ, 10-locular; Sierra Leone ..... *G. guineensis* Dodge
22. Ascospores 40–50 × 7–9 μ, 8–10-locular; thallus greenish white; lirellae 1–3 × 0.25 mm.; Usambara ..... *G. aterrima* Müll. Arg.
22. Ascospores 55 × 8 μ, 11–14-locular; thallus white, parathecium reddish black; Usambara ..... *G. erythrocardia* Müll. Arg.

Graphis Afzelii Ach., Syn. Lich. 85. 1814.

Dyplolabia Afzelii Mass., Neagenea Lich. 6. 1854.

Type: Guinea, corticole, Afzelius.

Thallus epiphloeodal, 75 μ thick, light brownish olive, without a black margin; cortex 25 μ thick, gelified, of periclinal, slender, thick-walled hyphae about 2 μ in diameter; algal layer 50 μ thick, of subvertical filaments of *Trentepohlia* about 4 μ in diameter; medulla not differentiated, but hyphae penetrating deeply between the bark cells. Lirellae straight, curved or flexuous, rarely once-forked, 2–3(–4) × 1 mm., about 0.3 mm. tall, densely white-pruinose, lips connivent, thalline cortex with an occasional algal cell extending halfway up the parathecium where it is replaced by a layer of slender vertical hyphae 4 μ in diameter, closely septate, somewhat gelified and decomposed, forming a layer about 80 μ thick; parathecium 80 μ thick above the thecium, expanding to 180 μ thick on the sides, narrowing abruptly at the level of the base of the thecium then expanding rapidly to 135 μ, making an acute angle with the bark and extending only slightly under the margin of the hypothecium, thus dimidiate, carbonaceous; hypothecium 25 μ thick, the lower half gelified, the upper half of deeply staining, densely woven, slender hyphae; thecium 90–105 μ tall; paraphyses slender, simple, tips not thickened; asci 8-spored, clavate, tips not thickened, 80–90 × 8–11 μ; ascospores ellipsoidal, 4-locular, 16 × 8 μ, terminal protoplasts spherical, central ones lenticular, connected by a very slender isthmus which is finally obliterated.

The shape of the parathecium is quite variable in cross-section in this species. The above description was based on *Deighton M4337*. In *Deighton M4408*, the lips are not so closely connivent, the thecium is wider, and the gelified layer of the hypothecium is 55–65 μ thick, slightly yellowish, resting on a thin, discontinuous layer of blackened bark cells. In Deighton M4629, the outer margin of the parathecium is not so conspicuously angled at the level of the base of the thecium. All collections cited agree closely in all other characters.

G. Afzelii differs from *G. nivea* Fée, Essai Crypt. Ecorces Officin. 47. 1824 (type from Peru on *Cinchona oblongifolia* Mutis), to which tropical American material should be referred instead of to *G. Afzelii*, in the thinner cortex and thallus, relatively thicker algal layer, lirellae dimidiate instead of entire and with a thinner base, lips not sulcate, broader and thinner parathecium, lower thecium and smaller asci and ascospores.

Sierra Leone: Njala (Kori), on *Peltophorum africanum* v. *speciosum*, F. C. Deighton M4337, on *Anisophyllea laurina*, F. C. Deighton M4408, on *Citrus aurantifolia*, F. C. Deighton M4629.

GRAPHIS **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Owena near Ondo, on *Theobroma*, C. A. Thorold 124.

Thallus epiphloeodes, ravus, 55 μ crassitudine, homoeomerus, filamentis verticalibus *Trentepohliae* 6 μ diametro et hyphis tenuibus intertextis cum crystallis ad 10 μ diametro. Lirellae flexuosae, usque ad 2 $\times$ 0.5 mm., simplices, labiis elevatis, subpruinosis, conniventibus mox delabentibus et discum pruinosum exponentibus; parathecium dimidiatum, superne 18–20 μ ad 25 μ in lateribus dilatatum, hyalinum vel pallide brunneum, hyphis tenuibus, septatis, 3–4 μ diametro, pseudoparenchyma formantibus; hypothecium 15 μ crassitudine, hyphis tenuibus dense contextum; thecium 65–70 μ altitudine, ad 360 μ latitudine; paraphyses tenues, simplices, apicibus non incrassatae; asci cylindrici, 65 $\times$ 12 μ; ascosporae octonae, imbricatim monostichae, hyalinae, 4-loculares, protoplastis terminalibus subconicis, centralibus rotundatis, ellipsoideae, 16 $\times$ 8 μ.

Thallus epiphloeodal, 55 μ thick, drab, cortex not differentiated; algal filaments of *Trentepohlia* about 6 μ in diameter, vertical and penetrating deeply between the bark cells; medulla not differentiated, but of slender, interwoven hyphae inclosing many hyaline crystals up to 10 μ in diameter between the algal filaments. Lirellae flexuous, up to 2 $\times$ 0.5 mm., unbranched, lips elevated, slightly pruinose, connivent, soon breaking away and exposing the pruinose disc; parathecium dimidiate, 18–20 μ thick above the thecium, up to 25 μ thick on the sides of the thecium, hyaline or pale brownish, of slender, septate hyphae 3–4 μ in diameter, forming a pseudoparenchyma; hypothecium 15 μ thick, of densely woven, deeply staining, slender hyphae; thecium 65–70 μ tall, 360 μ wide; paraphyses slender, unbranched, tips not thickened; asci cylindric, 8-spored, 65 $\times$ 12 μ; ascospores imbricately monostichous, hyaline, 4-locular, terminal protoplasts subconical, somewhat smaller than the rounded central ones, ellipsoidal, 16 $\times$ 8 μ.

GRAPHIS **Thoroldi** Dodge, sp. nov.

Type: Nigeria, Ina near Ibadan, on *Theobroma*, C. A. Thorold 151b.

Thallus epiphloeodes, laevis, 15–20 μ crassitudine, obscure olivaceo-griseus, homoeomerus, filamentis subverticalibus *Trentepohliae* 6–7 μ diametro. Lirellae rectae, 0.5–0.6 $\times$ 0.2 mm., emersae, nigrae, labiis conniventibus; parathecium integrum, carbonaceum, superne 15 ad 35 μ in lateribus et sub hypothecio dilatatum; hypothecium 15 μ crassitudine, hyphis tenuibus dense contextum; thecium 80 μ altitudine, 125 μ latitudine; paraphyses tenues apicibus subclavatis, brunneis; asci clavati, dein ellipsoideae, 55 $\times$ 16 μ; ascosporae octonae, hyalinae, 4-loculares, anguste ellipsoideae, 14–15 $\times$ 5–6 μ.

Thallus epiphloeodal, smooth, 15–20 μ thick, dark olive gray, homoeomerous, of subvertical, partly disorganized filaments of *Trentepohlia*, 6–7 μ in diameter, and slender hyphae, somewhat decomposed above, somewhat thicker near the

lirellae and disorganizing the cork cells to a depth of 80 μ, but the algae not penetrating between them. Lirellae straight, 0.5–0.6 $\times$ 0.2 mm., emersed, black, lips connivent; parathecium carbonaceous, entire, 15 μ thick at the lips, expanding to 35 μ on the sides and under the hypothecium, and blackening the cork cells to a depth of 55 μ below it; hypothecium 15 μ thick, of slender, densely woven hyphae; thecium 80 μ tall, 125 μ wide; paraphyses slender, tips slightly clavate, brownish in the epithecial gel, which is about 18 μ thick; asci clavate, becoming ellipsoidal, 8-spored, 55 $\times$ 16 μ; ascospores hyaline, 4-locular, 14–15 $\times$ 6 μ, narrowly ellipsoidal.

GRAPHIS **ondensis** Dodge, sp. nov.

Type: Nigeria, Ondo Province, Ipetu, on *Theobroma*, C. A. Thorold 120.

Thallus epiphloeodes, ad 55 μ crassitudine, laevis vel minute verrucosus, opacus, albidus; cortex 8 μ crassitudine, hyphis septatis periclinalibus, gelifactus, granulis minutis inspersus; stratum algarum 25 μ crassitudine, filamentis verticalibus *Trentepohliae* 5–6 μ diametro; medulla 22 μ crassitudine, hyphis tenuibus, magnis cum crystallis hyalinis. Lirellae emersae, 4 $\times$ 0.6 mm., curvatae vel flexuosae, margine sulcato, labiis conniventibus, thallo 40 μ crassitudine sine crystallis in medulla tectae; parathecium integrum, ad labias 15 μ, lateribus 230 μ, basi 80 μ crassitudine, cum 6–7 sulcis 60 μ altitudine, carbonaceum; hypothecium 25 μ crassitudine, hyphis tenuibus dense contextum; thecium cordiforme, 105 μ altitudine latitudineque; paraphyses tenues, pachydermeae, apicibus brunneis non incrassatis; asci cylindrici, 90 $\times$ 30 μ; ascosporae binae vel quaternae, hyalinae, 12-loculares, protoplastis rotundatis, pachydermeae, 80 $\times$ 14 μ.

Thallus epiphloeodal, up to 55 μ thick, smooth to minutely verrucose, surface dull, whitish; cortex 8 μ thick, gelified, of septate, periclinal hyphae inspersed with minute granules; algal layer about 25 μ thick, of loosely packed, vertical filaments of *Trentepohlia* 5–6 μ in diameter; medulla about 22 μ thick, of slender hyphae inclosing large hyaline crystals, penetrating about 35 μ into the cork cells but not disorganizing them. Lirellae emersed, about 4 $\times$ 0.6 mm., curved or flexuous, margin sulcate, lips connivent, covered by a layer of thallus 40 μ thick, but with few or no crystals in the medulla; parathecium entire, 15 μ thick at the lips, expanding to 230 μ thick on the sides and narrowing to 80 μ under the hypothecium, with 6–7 grooves extending about 60 μ deep, carbonaceous; hypothecium 25 μ thick, of slender, closely interwoven hyphae; thecium cordiform, 105 μ tall and broad; paraphyses slender, thick-walled, unbranched, tips brownish but not thickened; asci 2–4-spored, cylindric, 90 $\times$ 30 μ; ascospores about 12-locular, hyaline, protoplasts rounded, thick-walled, about 80 $\times$ 14 μ.

GRAPHIS **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Bauhinia tomentosa*, F. C. Deighton M4307E, M4307G.

Thallus epiphloeodes, albidus, anguste nigro-marginatus, 100 μ crassitudine; cortex decompositus, 8–10 μ crassitudine; stratum algarum 40 μ crassitudine,

filamentis verticalibus *Trentepohliae* 5–6 μ diametro; medulla 50 μ crassitudine, hyphis tenuibus laxe intertextis, magnis cum crystallis, ad cellulas suberosas magis compactis periclinalibusque. Lirellae rectae aut subcurvatae, 0.5 (1.8) mm. longitudine, semi-emersae, labiis conniventibus; parathecium dimidiatum, superne 15 μ, inferne usque ad 55 μ dilatatum, lateribus verticalibus non alatis, carbonaceum; hypothecium 15–20 μ crassitudine, hyphis tenuibus dense contextum; thecium 120 μ altitudine, 150 μ latitudine; paraphyses tenues, semel vel bis dichotome ramosae, apicibus subclavatis, cellula terminali 5–6 μ diametro; asci clavati dein subcylindrici, ca. 60 $\times$ 16 μ; ascosporae octonae, subclavatae, apice uno obtuso, altero magis acuto, 8–10-loculares, protoplastis lenticularibus, 30 $\times$ 8 μ.

Thallus epiphloeodal, whitish, narrowly black-margined, at least in contact with the thalli of other lichens, about 100 μ thick; cortex decomposed, 8–10 μ thick; algal layer 40 μ thick, of vertical filaments of *Trentepohlia* 5–6 μ in diameter; medulla 50 μ thick, of slender, loosely interwoven hyphae inclosing large, hyaline crystals, more compact and periclinal next the cork cells. Lirellae straight or slightly curved, 0.5 (–1.8) $\times$ 0.26 mm., semi-emersed, lips black, connivent; parathecium dimidiate (sometimes the outermost bark cells are blackened, then appearing entire but thinner at the base in thick sections), 15 μ thick above, expanding to 55 μ at the base, sides vertical, not winged at the base, carbonaceous; hypothecium 15–20 μ thick, seated on the yellowish to blackened bark cells, of slender, densely woven hyphae; thecium 120 μ tall, 150 μ broad; paraphyses slender, once or twice dichotomously branched, tips clavate, terminal cells brownish, 5–6 μ in diameter; asci clavate, becoming subcylindric, about 60 $\times$ 16 μ, 8-spored; ascospores hyaline, 8–10-locular, subclavate, one end obtuse, the other more acute, protoplasts lenticular, 30 $\times$ 8 μ.

GRAPHIS **guineensis** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Lagerstroemia speciosa*, F. C Deighton M4345.

Thallus epiphloeodes, ca. 25 μ crassitudine, laevis, pallide cinereus vel albidus; cortex 15 μ crassitudine, gelifactus, hyphis periclinalibus; stratum algarum ca. 10 μ crassitudine, filamentis periclinalibus *Trentepohliae* 5–6 μ diametro. Lirellae curvatae, 2 $\times$ 0.13 mm., rare furcatae, emersae, labiis conniventibus; parathecium dimidatum, carbonaceum, superne 15 μ, ad 35 μ inferne dilatum, basi subalatum; hypothecium 20 μ crassitudine, hyphis tenuibus dense contextum; thecium subcordiforme, 55 μ altitudine, 95 μ latitudine; paraphyses tenues, simplices; asci cylindrici; ascosporae octonae, curvatae, 10-loculares, 27 $\times$ 7–8 μ.

Thallus epiphloeodal, about 25 μ thick, margin indefinite, smooth, pale ashy to white; cortex 15 μ thick, gelified, of periclinal hyphae; algal layer about 10 μ thick, of periclinal filaments of *Trentepohlia* 5–6 μ in diameter, some penetrating between the bark cells; medulla not differentiated. Lirellae curved, up to 2 $\times$ 0.16 mm., some forked, emersed, lips connivent, black, sides covered with thallus; parathecium dimidiate, carbonaceous, lips 15 μ thick, sides 35 μ thick, very slightly

angled at the base; hypothecium 20 μ thick, of slender, densely woven hyphae; thecium subcordate, 55 μ tall, 95 μ wide; paraphyses slender, unbranched; asci 8-spored, cylindric; ascospores curved, 10-locular, 27 $\times$ 7–8 μ.

PHAEOGRAPHIS

PHAEOGRAPHIS Müll. Arg., Flora 65:336. 1882.

Leiorreuma Eschw., Syst. Lich. 14. 1824.
Pyrochroa Eschw., Syst. Lich. 15. 1824.
Platygramma Meyer, Nebenstudien, 332. 1825.
Leiogramma Eschw. in Martius, Icon. Pl. Crypt. Brasil. 2:11. 1828.
Graphidula Norm., Nyt Mag. Naturvidensk. 7:240. 1853.
Hymenodecton Leight., Ann. Mag. Nat. Hist. II, 13:387. 1854.
Chiographa Leight., Ann. Mag. Nat. Hist. II, 13:388. 1854.
Solenographa Mass., Atti I. R. Ist. Veneto III, 5:270. 1860.
Pyrrhographa Fée in Mass., Atti I. R. Ist. Veneto III, 5:272. 1860.
Theloschisma Trev., Conspect. Verruc. 14. 1860.

Type: none designated for *Phaeographis* Müll. Arg. *Leiorreuma* Eschw. was based on *Opegrapha Lyellii* Sowerby now in *Phaeographis*. When Eschweiler included *Leiorreuma* as a section of his *Leiogramma* in 1828, he added *Graphis scalpturata* Ach., now in *Phaeographina*, and *L. tartareum* Eschw., now in *Opegrapha*. In his section *Lecanactis* of *Leiogramma*, he included *L. sericeum* and *L. punctiforme* (both now in *Phaeographis*) and *L. pruinosum* (now in *Helminthocarpon*). *Pyrochroa* Eschw. was based on *Graphis coccinea* Holl and *P. flammula* Eschw., both now in *Phaeographis*, and *Graphis caribaea* Ach., now in *Arthonia*. *Platygramma* Meyer included *P. dendriticum*, *P. Lyellii* (both now in *Phaeographis*), and *P. suffultum* (now in *Phaeographina*). *Graphidula* Norm. is a *nomen nudum*, as no type was designated, nor new combinations made. *Hymenodecton* Leight. was based on *Graphis dendritica* Ach. *Chiographa* Leight. was based on *Opegrapha Lyellii* Sowerby. *Solenographa* Mass. was based on *Lecanactis confluens*, now in *Phaeographis*. *Pyrrhographa* Fée was based on *Pyrochroa flammula* and *P. medusulina*, both now in *Phaeographis*, and *P. javanica*, now in *Graphina*. *Theloschisma* was based on *T. Eschweileri* (Mont.) Trev. (*Verrucaria aspistea* Eschw. *non* Ach.).

From the above synonymy, it is obvious that many names antedate *Phaeographis* Müll. Arg. Since the latter name has been in constant use by most lichenologists for the last seventy years, a type species should be chosen and *Phaeographis* should be conserved, but without prejudice against older names if the genus is divided. There are several groups of species, now in *Phaeographis*, which differ in important characters and should be segregated as genera. It would be unfortunate, however, if this were done without a thorough study of the species from all regions. Until such a monograph is published, it seems wise to continue the use of *Phaeographis* for all Graphidaceae with brown, septate ascospores except those now placed in *Melaspilea*.

Thallus crustose, epi- or endophloeodal; ecorticate or with a cortex of periclinal hyphae; algae *Trentepohlia*. Lirellae immersed to sessile, elongate or branched, rarely short and rounded, lips connivent or open, entire or sulcate; parathecium entire or dimidiate, carbonaceous or subhyaline; hypothecium thin, hyaline; paraphyses slender, unbranched, tips not conspicuously clavate; asci clavate to subcylindric, 4–8-spored; ascospores brown, fusiform to ellipsoid or subcylindric, septate, protoplasts lenticular to subspherical; spermatia exobasidial, cylindric, relatively long (rarely observed).

1. Parathecium pale; ascospores 4-locular, 13–16 × 6 μ; lirellae oblong-difform, disc open, black, margin densely pruinose; São Thomé.....*P. subnivescens* (Nyl.) Zahlbr.
1. Parathecium black 2
2. Parathecium entire 3
2. Parathecium dimidiate 11
3. Parathecium thicker below, lips connivent, sulcate 4
3. Parathecium not conspicuously thicker below.....5
4. Ascospores 8–12-locular, 38–46 × 9–11 μ; on palm wood; Tanganyika.....*P. palmarum* Müll. Arg.
4. Ascospores 4-locular, 27–30 × 7–8 μ; corticole; Sierra Leone.....*P. Deightoni* Dodge
5. Lips connivent, disc very narrow; lirellae prominent, simple or slightly branched.....6
5. Lips widely divergent 8
6. Ascospores 4-locular; Mozambique 7
6. Ascospores 10–12-locular, 55–65 × 8–10 μ; lirellae orange-pruinose; Cameroons.....*P. ochracea* Dodge
6. Ascospores 16-locular, 85 × 15 μ; lirellae white-pruinose at first, soon nude and black; Sierra Leone .....*P. sierraleonensis* Dodge
7. Ascospores 16 × 7 μ; thallus K—.....*P. micrographa* (Vainio) Zahlbr.
7. Ascospores 18.2–23 × 6.5–7.5 μ; thallus K reddening.....*P. tigrinella* (Vainio) Zahlbr.
8. Lirellae innate, branched; ascospore size not given; Liberia.....*P. dendriticella* Müll. Arg.
8. Lirellae rounded, ellipsoid to oblong, not branched.....9
9. Foliicole; ascospores 6-locular, 20–22 × 6–7 μ; Angola.....*P. Phyllocharis* (Vainio) Zahlbr.
9. Corticole 10
10. Thallus endophloeodal; lirellae prominent, 0.3–1.5 × 0.2–0.3 mm., disc black or slightly pruinose; ascospores 6-locular, 18–28 × 6–7 μ; Angola.....*P. sexlocularis* (Vainio) Zahlbr.
10. Thallus thin, verrucose, shining, whitish; lirellae innate, 1–1.5 × 0.15–0.2 mm., disc not pruinose; ascospores 15.5–27 × 7–7.5 μ; Mozambique.....*P. subdevelans* (Vainio) Zahlbr.
11. Lips sulcate or striolate; ascospores 6-locular, 20 × 7.5 μ; Usambara.....*P. duplicans* Müll. Arg.
11. Lips striolate; ascospores 6-locular, 25 × 8–9 μ; lirellae 0.7 mm. broad, 2–3-furcate; Usambara .....*P. platycarpa* Müll. Arg.
11. Lips not sulcate or striolate, entire.....12
12. Ascospores 12 or more locular, 100–105 × 13 μ; asci 4-spored; lirellae covered by thallus, 3 mm. long, unbranched; Sierra Leone.....*P. tecta* Dodge
12. Ascospores 6–8-locular 13
12. Ascospores 4-locular 14
13. Lirellae simple or sparingly branched, 0.5–2.5 × 0.2 mm.; ascospores 6-locular, 20–30 × 6–8 μ; Angola .....*P. navicularis* (Vainio) Zahlbr.
13. Lirellae simple, 0.5–2 × 0.2–0.25 mm.; ascospores 6–8-locular, 23–26 × 6.5–7.5 μ; Congo .....*P. paragrapta* Müll. Arg.
13. Lirellae radially branched, immersed, 1–1.5 × 0.2 mm., disc open, pruinose; ascospores 28–38 × 9 μ; Socotra.....*P. inusta* v. *radians* Müll. Arg.
14. Lirellae simple or sparingly branched, immersed.....15
14. Lirellae dichotomously and partly radially branched, 1–4 × 0.1 mm., subimmersed; Mozambique 16
15. Lirellae simple or sparingly branched, 0.2–2.5 × 0.1–0.5 mm.; ascospores 9–16 × 4–7 μ; lignicole; Mozambique .....*P. lignatilis* (Vainio) Zahlbr.
15. Lirellae simple, white-pruinose; ascospores 14–18 × 6 μ; corticole; São Thomé.....*P. lynceodes* (Nyl.) Zahlbr.
16. Ascospores 17–19 × 6–8 μ.....*P. micrographoides* (Vainio) Zahlbr.
16. Ascospores 21 × 8 μ.....*P. leucothallina* (Vainio) Zahlbr.

PHAEOGRAPHIS **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Amphimas pterocarpoides*, F. C. Deighton M4334A.

Thallus endophloeodes, albidus. Lirellae rectae, subfusiformes, sessiles, 1 × 0.25 mm., nigrae, labiis conniventibus, sulcatis; parathecium integrum, carbonaceum, basi 185 μ crassitudine, in lateribus ad 55 μ tenuescens; thecium 135 μ altitudine; paraphyses tenues, apicibus non incrassatis; asci clavati; ascosporae octonae, distichae, 4-loculares, brunneae, rectae vel subcurvatae, ellipsoideae vel subfusiformes, 27–30 × 7–8 μ.

Thallus endophloeodal, whitish, consisting of a few *Trentepohlia* cells and hyphae between the partly disorganized bark cells, making the surface silvery-ashy. Lirellae straight, subfusiform, sessile, about 1 × 0.25 mm., black, lips connivent, somewhat sulcate-striate; parathecium entire, carbonaceous, 185 μ thick below, thinning to 55 μ thick on the sides; thecium 135 μ tall; paraphyses slender, tips not thickened; asci 8-spored, clavate; ascospores distichous, ellipsoid to subfusiform, brown, straight or slightly curved, 4-locular, 27–30 × 7–8 μ.

PHAEOGRAPHIS **ochracea** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Bauhinia tomentosa*, F. C. Deighton M4307G.

Thallus epiphloeodes, 80 μ crassitudine, minute verrucosus, nitidus, pallide olivaceo-griseus; cortex 25–30 μ crassitudine, hyphis periclinalibus, 3 μ diametro, gelifactis; stratum algarum 50–55 μ crassitudine, filamentis verticalibus *Trentepohliae* 3–4 μ crassitudine, magnis cum crystallis; medulla non evoluta. Lirellae sessiles, rectae vel subcurvatae, rarissime dichotome ramosae, 1–2.5 × 0.5 mm., labiis conniventibus, obscure sulcatis, aurantiaco-pruinosis; parathecium dimidiatum, carbonaceum, 15–30 μ crassitudine ad labias, 30–45 μ ad latera, usque ad 185 μ in alis dilatatum; thecium cordiforme, 80–105 μ altitudine latitudineque; paraphyses tenues, apicibus non incrassatis, sed cum crystallis brunneis; asci clavati dein ellipsoidei, 100 × 25 μ; ascosporae octonae, subcylindrici, brunneae, 10–12-loculares, 55–65 × 8–10 μ.

Thallus epiphloeodal, 80 μ thick, minutely verrucose, shining, pale olive gray; cortex 25–30 μ thick, of gelified periclinal hyphae 3 μ in diameter; algal layer 50–55 μ thick, of disorganized, vertical filaments of *Trentepohlia* 3–4 μ in diameter, with very large hyaline crystals (such as one sees in the Thelotremaceae). Lirellae sessile, straight or slightly curved, very rarely once-forked, 1–2.5 × 0.5 mm., lips connivent, very obscurely sulcate, covered by cortex at first, then the cortex cracking away, exposing powdery orange material about the parathecium; amphithecium consisting of thalline cortex and alcohol-soluble, orange material which replaces the algal layer on the sides of the parathecium, but not extending into the thallus proper; parathecium dimidiate, carbonaceous, about 15–30 μ thick at the lips, 30–45 μ on the sides and expanding to 185 μ where it makes an acute angle with the bark cells which are sometimes blackened to a depth of 55 μ below

the thecium (thus giving the appearance of an entire parathecium); thecium cordiform, 80–105 μ tall and broad; paraphyses slender, tips not thickened but the epithecium covered with brownish crystals; asci 100 $\times$ 25 μ, clavate, becoming ellipsoidal, 8-spored; ascospores subcylindric, 55–65 $\times$ 8–10 μ when pale brown, 9–11-septate, shrinking to 30 $\times$ 6 μ when very dark brown.

After the thecium has partly disintegrated, a new thecium forms below the old hypothecium (seen in most of the lirellae sectioned in *Thorold 121*). As the new parathecium expands, the old parathecium breaks away at the junction with the new parathecium, the scars leaving the new parathecium shallowly sulcate when this has been repeated about four or more times, as the new parathecium is covered by a new outgrowth of the thallus to form each new parathecium. Only a single, shrunken but very dark brown spore was found in *Thorold 121* after repeated sectioning of various lirellae, but the other structures agree well with those of the Sierra Leone material.

Sierra Leone: Njala (Kori), on *Bauhinia tomentosa*, F. C. Deighton M4307G.
Cameroons: Tombel, on *Theobroma*, C. A. Thorold 121.

PHAEOGRAPHIS **sierraleonensis** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twig of *Bauhinia tomentosa*, F. C. Deighton M4307Ga.

Thallus epiphloeodes, 70–80 μ crassitudine, minutissime verrucosus, pallide olivaceo-griseus; cortex 25 μ crassitudine, decompositus, hyphis periclinalibus gelifactus; stratum algarum 45–55 μ crassitudine, filamentis verticalibus *Trentepohliae* 6–7 μ diametro; medulla non evoluta. Lirellae usque ad 2 $\times$ 0.4 mm., rectae vel flexuosae, elevatae, juventute cortice thallino tecta, dein nudae, nigrae; labiis conniventibus; parathecium integrum, carbonaceum, superne 15 μ crassitudine, in lateribus 120 μ et sub hypothecio 80 μ, margine subalato; hypothecium 20 μ crassitudine, hyphis tenuibus dense contextum; thecium 160 μ altitudine, 200 μ latitudine; paraphyses tenues, super ascos dichotome ramosae, cellulis ultimis clavatis vel rotundatis, 3 μ diametro, crystallis subbrunneis minutis tectis; asci clavati dein ellipsoidei, 100 $\times$ 40 μ; ascosporae octonae?, 16-loculares, protoplastis rotundatis, brunneae, 85 $\times$ 15 μ.

Thallus epiphloeodal, 70–80 μ thick, very minutely verrucose, light olive gray; cortex 25 μ thick, decomposed, of predominantly periclinal, gelified hyphae; algal layer 45–55 μ thick, of vertical filaments of *Trentepohlia* 6–7 μ in diameter; medulla not differentiated. Lirellae up to 2 $\times$ 0.4 mm., straight or flexuous, unbranched, elevated, covered by a thin thalline cortex when young, finally nude and black in the upper portion; lips connivent; parathecium entire, carbonaceous, 15 μ thick at the lips, expanding to 120 μ on the sides and 80 μ thick below the hypothecium, slightly winged; hypothecium 20 μ thick, of slender, densely woven hyphae; thecium 160 μ tall, 200 μ broad; paraphyses slender, once or twice dichotomous above the asci, terminal cells clavate to subspherical, 3 μ in diameter, covered with minute brownish crystals; asci clavate, becoming ellipsoidal, 8-

spored?, 100 × 40 μ; ascospores long remaining hyaline, finally becoming brown, 16-locular, protoplasts somewhat rounded, about 85 × 15 μ.

PHAEOGRAPHIS **tecta** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Bauhinia tomentosa*, F. C. Deighton M4307 pro parte minore.

Thallus epiphloeodes, 40 μ crassitudine, albidus; cortex gelifactus, 15 μ crassitudine, hyphis periclinalibus; stratum algarum 25 μ crassitudine, filamentis *Trentepohliae* periclinalibus ca. 6 μ diametro; medulla non evoluta. Lirellae ad 3 × 0.4 mm., flexuosae, strato thallino tectae, labiis conniventibus; parathecium carbonaceum, dimidiatum, ad labias 30 μ crassitudine, lateribus ad 150 μ, extus intusque alatae; hypothecium centro 25 μ crassitudine ad margines tenuescens, hyphis tenuibus dense contextum; thecium cordiforme, 130 μ altitudine, 180 μ latitudine, dein rotundatum; paraphyses tenues, super ascos dichotome ramosae, cellulis terminalibus clavatis, brunneis, 4 μ diametro; asci ellipsoidei, 105 × 27 μ; ascosporae quaternae, brunneae, 12- aut pluri-loculares, protoplastis lenticularibus 100–105 × 13 μ.

Thallus epiphloeodal, whitish, about 40 μ thick; cortex gelified, 15 μ thick, of periclinal hyphae; algal layer 25 μ thick, of loosely arranged, periclinal filaments of *Trentepohlia* about 6 μ in diameter; medulla not differentiated. Lirellae up to 3 × 0.4 mm., flexuous, completely covered by a thin layer of thallus, lips connivent; parathecium carbonaceous, dimidiate, 30 μ thick above the thecium expanding to 150 μ at the base in contact with the bark cells, angled both without and within; hypothecium 25 μ thick in the center, thinning toward the margin, of deeply staining, densely interwoven hyphae; thecium cordiform then rounded, 130 μ tall, 180 μ wide; paraphyses slender, dichotomous above the asci, terminal cells clavate, brown, 4 μ in diameter; asci 4-spored, ellipsoidal, 105 × 27 μ; ascospores finally brownish, 12 or more locular, protoplasts lenticular, 100–105 × 13 μ.

In very old lirellae, the thallus and tops of the lips weather away, exposing the narrow disc, and the tops of the lirellae appear somewhat pruinose. Below the hypothecium, one or two layers of bark cells are blackened, giving the appearance of an entire parathecium with a very thin base in thick sections. Apparently the browning of the spore occurs late, so that nearly mature spores might be looked for in *Graphis*.

PHAEOGRAPHIS LYNCEODES Zahlbr., Cat. Lich. Univ. 2:381. 1923.

Graphis lynceodes Nyl., Flora 69:174. 1886.

Type: São Thomé, Bom Successo, 1150 m., corticole, A. Moller, comm. Henriques.

Thallus epiphloeodal, about 65 μ thick, deep olive buff; cortex 25 μ thick, of compact, more or less vertical, slender hyphae, the outer 6 μ partly decomposed, with abundant minute crystals; algal layer of *Trentepohlia* filaments about 6 μ in diameter, more or less periclinal, rather few; medulla of slender, loosely woven hyphae with lacunae, in other portions more densely woven. Lirellae variable in

shape, mostly short and rounded, often confluent in somewhat curved lines, margin and open disc densely but minutely white-pruinose, immersed or nearly so; parathecium dimidiate, about 10 μ thick, not wider at the base, deep brown; hypothecium poorly developed, about 6 μ thick; thecium 55–60 μ tall; paraphyses slender, unbranched, tips not thickened; asci broadly clavate, about 40 $\times$ 8 μ, walls slightly thickened when young, 8-spored; ascospores early pale brown, 4-locular, protoplasts somewhat rounded, 14–18 $\times$ 5–6 μ.

In the lirella sectioned, cell division of the ascospore is slower and less synchronous than is usual in the Graphidaceae. Even after the ascospores in the ascus have begun to turn brown and they have reached nearly the mature size, both 2-locular and 3-locular ones may be observed. The systematic position of this species is somewhat doubtful. Nylander states that it is close to *Graphis (Phaeographis) inusta* in the *G. (Phaeographis) dendritica* group. Our material, though scant, agrees closely with Nylander's description except for hyaline spores.

Cameroons: Tombel, on *Theobroma*, C. A. Thorold 136, growing with *Pyrenula heteroclita* Ach., *P. mamillana* (Ach.) Trev., and *Sarcographa labyrinthica* (Ach.) Müll. Arg.

GRAPHINA

GRAPHINA Müll. Arg., Flora 63:22. 1880.
Diorygma Eschw., Syst. Lich. 13. 1824.
Leucogramma Meyer, Nebenstudien, 331. 1825.
Hemithecium Trev., Spighe e Paglie, 12. 1853.
Thalloloma Trev., Spighe e Paglie, 13. 1853.
Glaucinaria Mass., Atti I. R. Ist. Veneto III, 5:319. 1860.
Stenographa Mudd, Man. Brit. Lich. 235. 1861.

Type: not designated. *Diorygma* Eschw. was based on *D. tinctorum* Eschw. (figured). *Leucogramma* Meyer was based on *L. turgidum, L. plicatum, L. confertum, L. serpentarium, L. raddacense* and *L. carneum*, all placed as *species dubiae* in *Graphina* by Zahlbruckner; none of them have been reported since the original descriptions in Sprengel, Syst. Veg. 4:2:327. 1827. *Hemithecium* Trev. was based on six species, of which all but *H. chrysenteron* (Mont.) Trev. remain in *Graphina* as now used. *Thalloloma* Trev. and *Stenographa* Mudd were both based on *Ustalia anguina* Mont. *Glaucinaria* Mass. was based on *Graphis Poitiaei* Fée, *G. hololeuca* Mont., *G. Junghuhnii* Mont., and *G. raddacensis* Meyer.

From the above synonymy, it is evident that we have a case parallel to that of *Phaeographis* with many names antedating *Graphina* Müll. Arg., although the latter has been in general use since its publication. In the same way, a type species should be chosen and *Graphina* Müll. Arg. conserved without prejudice against older names, if the genus is divided.

Thallus crustose, epi- or endophloeodal, ecorticate or with a cortex of longitudinal hyphae; algae *Trentepohlia*. Lirellae immersed to sessile, elongate or branched, lips connivent to open, entire or sulcate; parathecium entire or dimidiate,

carbonaceous to hyaline; hypothecium thin, hyaline; paraphyses slender, unbranched; asci cylindric to somewhat rounded; 1–8-spored; ascospores muriform, hyaline, protoplasts rounded.

1. Lirellae radiately branched, lips connivent; parathecium not described; ascospores 25–27 × 8–11 μ, 6–8-locular, 2–3-locellate; asci 6–8-spored; thallus thin; Cormoro Archipelago ..... *G. abstracta* (Krmplhbr.) Müll. Arg.
1. Lirellae simple or very sparingly branched 2
   2. Lirellae immersed or nearly so 3
   2. Lirellae emersed to sessile 5
      3. Asci 6–8-spored; ascospores 16–23 × 9–12 μ, 4–6-locular, 2-locellate; lateral parathecium thin, olive fuscous; Zanzibar coast ..... *G. pyrenuloidea* Müll. Arg.
      3. Asci 4-spored; ascospores 80 × 22 μ, 20-locular, 10-locellate; parathecium absent; Sierra Leone ..... *G. arthothelioides* Dodge
      3. Asci 4-spored; ascospores 96–100 × 36 μ, 28-locular, 6–8-locellate; parathecium fulvous, entire, lips connivent, sulcate; Sierra Leone ..... *G. Deightoni* Dodge
      3. Asci monosporous; parathecium pale, lips open 4
         4. Ascospores 70–85 μ long; lirellae 3–4 × 0.3 mm.; Abyssinia ..... *G. aethiopica* Müll. Arg.
         4. Ascospores 75–106 × 30–44 μ; lirellae 0.2–2 × 0.15–0.25 mm.; thallus 300–600 μ thick; Angola ..... *G. ulcerata* (Vainio) Zahlbr.
   5. Parathecium entire 6
   5. Parathecium dimidiate or base hyaline; asci 1–2-spored 8
   5. Parathecium scarcely developed; thallus pale clay, subpulverulent; asci 2–6-spored; ascospores 27–40 × 13–16 μ, 6–10-locular, 3–4-locellate; Socotra ..... *G. socotrana* Müll. Arg.
      6. Parathecium greenish or pale fuscescent; thallus ashy olive, tuberculate, sorediose; asci 8-spored; ascospores 25–35 × 10 μ, finally brown; Angola (probably belongs in *Phaeographina*) ..... *G. sorediella* Müll. Arg.
      6. Parathecium darker; thallus not sorediose; asci 1–4-spored 7
         7. Parathecium fuscous-rufous or paler; lips open; lirellae 0.7–2.5 × .06–0.7 mm.; ascospores solitary, 110–150 × 25–40 μ; Angola ..... *G. straminea* (Vainio) Zahlbr.
         7. Parathecium fulvous, lips connivent; lirellae 3 × 1 μ; asci 4-spored; ascospores 96–100 × 36 μ; Sierra Leone ..... *G. Deightoni* Dodge
         7. Parathecium black; thallus white, wrinkled; ascospores solitary, 66–120 × 21–23 μ; Ilha Principe ..... *G. rudescens* (Nyl.) Zahlbr.
            8. Lips sulcate, black above, paler below; thallus pale ochre; ascospores 80–120 × 28–34 μ; Usambara ..... *G. Brunnthaleri* Zahlbr.
            8. Lips entire, thallus ashy white 9
               9. Ascospores 23–26 × 8 μ, 8-locular, 2–3-locellate; lirellae 0.7–1 × 0.25–0.3 mm.; Socotra ..... *G. varians* Müll. Arg.
               9. Ascospores 30–68 × 14–22 μ 10
               9. Ascospores 100 × 25 μ; lirellae 1–2.5 × 0.3 mm.; Usambara ..... *G. subbiascens* Müll. Arg.
                  10. Lirellae 0.8–1.25 × 0.2–0.25 mm.; ascospores 60–68 × 16–18 μ (90–110 × 21–32 μ when solitary); Kenya ..... *G. heterospora* Steiner
                  10. Lirellae 0.7–3 × 0.25–0.5 mm.; ascospores 30–60 × 14–22 μ; Mozambique ..... *G. Pelletieri* v. *macrior* (Vainio) Zahlbr.
                  10. Lirellae 2–6 × 0.3–0.4 mm.; ascospores 54–65 × 14–16 μ; Angola ..... *G. ambrizensis* (Vainio) Zahlbr.

Graphina **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Citrus aurantifolia*, F. C. Deighton M4630.

Thallus epiphloeodes, cartilagineus, 200 μ crassitudine (usque ad 575 μ circa parathecium), obscure griseo-olivaceus; cortex 80–95 μ crassitudine, hyphis verticalibus dense intertextis, partim decompositus et minutis cum granulis obscuris nubilatus; stratum algarum 55 μ crassitudine, discontinuus, filamentis verticalibus *Trentepohliae* 7–8 μ diametro, cellulis brevibus, subrotundatis; medulla 50–65 μ crassitudine, hyphis periclinalibus, tenuibus, dense contexta. Lirellae rectae vel subcurvatae, 3 × 1 mm., labiis conniventibus, pluries sulcatis; parathecium in-

tegrum, fulvum, labia intima 105 μ crassitudine, fulva, pallidiori ad thecium; thecium 270 μ altitudine; paraphyses tenues, apicibus non incrassatis; asci subcylindrici, 245 $\times$ 32 μ; ascosporae quaternae, subdistichae, hyalinae, 28-loculares, 6–8-locellatae, 96–100 $\times$ 36 μ.

Thallus epiphloeodal, cartilaginous, margin indefinite, 200 μ thick (up to 575 μ thick next the parathecium), deep grayish olive; cortex 80–95 μ thick, of densely woven, predominantly vertical hyphae, the outer 20 μ partly decomposed and nubilated with minute, dark granules; algal layer about 55 μ thick, somewhat discontinuous, of short, mostly vertical filaments of *Trentepohlia* 7–8 μ in diameter, cells short and somewhat rounded; medulla 50–65 μ thick, of densely woven, slender hyphae, mostly periclinal, containing some disorganized bark cells. Lirellae straight to somewhat curved, about 3 $\times$ 1 mm., tilleul buff, lips connivent, several times sulcate in older lirellae; parathecium entire, innermost lip fulvous, 105 μ thick, paler next the thecium; thecium 270 μ tall; paraphyses slender, tips not thickened; asci subcylindric, about 4-spored, 245 $\times$ 32 μ; ascospores subdistichous, hyaline, about 28-locular, 6–8-locellate, 96–100 $\times$ 36 μ when free from the ascus.

GRAPHINA ULCERATA Zahlbr., Cat. Lich. Univ. 2:429. 1923.

Graphis ulcerata Vainio, Cat. Welwitsch Afric. Pl. 2:438. 1901.

Type: Angola, Golungo Alto, Cungulungulo, corticole, Welwitsch 245.

Thallus epiphloeodal, rimose subareolate, tea green, 300–600 μ thick (only 200 μ thick in our material); cortex scarcely differentiated, decomposed, about 5 μ thick; algal layer about 40 μ thick, of *Trentepohlia,* cells about 5–6 μ in diameter, filaments disorganized in a rather compact tangle of slender hyphae; medulla about 165 μ thick, very loosely woven, with some disorganized bark cells in the lower portion. Lirellae immersed, rounded or elongate, mostly curved and forked, 0.2–2 $\times$ 0.15–0.25 mm., covered by the thallus when young, then lips spreading and disc open at maturity; disc chalky white, pruinose, plane, level with the thalline margin; parathecium entire, about 30 μ thick, tawny, of thick-walled hyphae; hypothecium about 30 μ thick, of slender, densely woven, deeply staining hyphae; thecium 105–110 μ tall; paraphyses slender, unbranched, tips not thickened but covered by a tawny granular material in the upper 10 μ; asci clavate at first, becoming ellipsoid, monosporous, about 100 $\times$ 25 μ (immature); ascospores hyaline, about 20-locular, 6-locellate, 75–106 $\times$ 35–44 μ when free from the ascus.

Our specimens have a somewhat thinner thallus with most ascospores nearer the lower limits of the size given by Vainio.

Nigeria: Ina near Ibadan, on *Theobroma,* C. A. Thorold 119.

Sect. **Platygrammodes** Dodge, sect. nov.

Type: *Graphina arthothelioides* Dodge, the only species known so far.

Lirellae innatae, disco primo a thallo tecto, dein aperto; parathecio nullo.

Lirellae innate at first, covered by a thin layer of thallus, disc finally open and level with the thallus; parathecium absent.

The complete absence of the parathecium separates this section from all others in the genus. Perhaps it is closest to the dimidiate sect. *Platygrammina* Müll. Arg. and the entire sect. *Platygraphina* Müll. Arg., in both of which the pale parathecium is less well developed than in the other sections. *Platygrammodes* bears the same relation to *Platygrammina* that the Lecanoraceae bear to the Lecideaceae. The complete absence of parathecium suggests *Arthothelium* of the Arthoniaceae, but all the structures of the thecium are clearly those of *Graphina*.

GRAPHINA **arthothelioides** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Bauhinia tomentosa*, F. C. Deighton M4307F.

Thallus epiphloeodes, pruinosus, 130 μ crassitudine, pallide griseus; ecorticatus; stratum algarum 40 μ crassitudine, filamentis *Trentepohliae* 3–4 μ diametro, cellulis cylindricis vel subellipsoideis; medulla gelifacta, hyphis 2 μ diametro laxe intertexta. Lirellae orbiculares vel oblongae, rectae vel curvatae, usque ad 2 $\times$ 0.5 mm., ex thallo erumpentes, disco pruinoso pallide alutaceo; parathecium verum non evolutum; hypothecium 13 μ crassitudine, parce evolutum; thecium 120 μ altitudine; paraphyses tenues, apicibus non incrassatis; asci clavati dein ellipsoidei, 170 $\times$ 28 μ; ascosporae juventute quaternae sed maturae binae, hyalinae, ellipsoideae, 20-loculares, 10-locellatae, 80 $\times$ 22 μ.

Thallus epiphloeodal, margin indefinite, pruinose, about 130 μ thick, light mineral gray; ecorticate; algal layer 40 μ thick, with occasional cells deep in the medulla, cells varying from cylindric to subellipsoid, the filaments of *Trentepohlia* curved and partly disorganized, 3–4 μ in diameter; medulla 90 μ thick, highly gelified, with loosely woven hyphae about 2 μ in diameter. Lirellae round to oblong, straight or curved, up to 2 $\times$ 0.5 mm., erumpent from the thallus, covered by a thin layer of thallus which finally peels off, leaving an open, flat, pruinose, pale buff disc level with the surrounding thallus; true lips and parathecium not differentiated; hypothecium about 13 μ thick, scarcely differentiated; thecium 120 μ tall; paraphyses slender, tips not thickened; asci clavate at first, becoming ellipsoid at maturity, 107 $\times$ 28 μ, 4-spored at first but usually two ascospores abort, leaving only two mature ascospores; ascospores hyaline, ellipsoid, muriform, 20-locular, 10-locellate, 80 $\times$ 22 μ.

PHAEOGRAPHINA

PHAEOGRAPHINA Müll. Arg., Flora 65:398. 1882.

Thecaria Fée, Essai Crypt. Ecorces Officin. 97. 1824.
Ectographa Trev., Spighe e Paglie, 11. 1853.
Thelographis Nyl., Mém. Soc. Sci. Nat. Cherbourg 5:130. 1857, *nom. nud.*
Megalographa Mass., Atti I. R. Ist. Veneto III, 5:317. 1860.
Thecographa Mass., Atti I. R. Ist. Veneto III, 5:316. 1860.
Pliarona Mass., Atti I. R. Ist. Veneto III, 5:318. 1860.
Leucogramma Mass., Atti I. R. Ist. Veneto III, 5:320. 1860, *non* Meyer, 1825.

Creographa Mass., Verhandl. K. K. Zool.-bot. Ges. Wien 10:686. 1860.
Leiorreuma Mass., Atti I. R. Inst. Veneto III, 5:319. 1860, non Eschw., 1824.

Type: not designated. *Thecaria* Fée was based on *T. quassiaecola* Fée (now in *Phaeographina*). *Ectographa* Trev. was based on *Graphis scalpturata* Ach. (now in *Phaeographina*) and *Opegrapha Poitiaei* Fée (now in *Graphina*). *Thelographis* Nyl. was based on *Graphis polymorpha* Fée. *Megalographa* Mass. was based on M. *hysterina* Mass. *Thecographa* Mass. was based on *T. ceramia* Mass. (now in *Phaeographina*). *Pliarona* Mass. was based on *Graphis Montagnei* v. d. Bosch (now in *Phaeographina*). *Leucogramma* Mass., *non* Meyer, was based on *Graphis chrysenteron* Mont. (now in *Phaeographina*). *Creographa* Mass. was based on C. *brasiliensis* Mass. (now in *Phaeographina*). *Leiorreuma* Mass., *non* Eschw., was based on *Opegrapha sordida* Fée, O. *depressa* Mont. & v. d. Bosch, O. *streblocarpa* Bél., and *Graphis scalpturatum* Ach., the last two transferred to *Phaeographina* by Müller Argau, the rest probably incorrectly transferred to *Graphina* by Zahlbruckner, as Massalongo states the muriform ascospores finally become brown.

From the above synonymy, it is evident that we have a case parallel to those of *Phaeographis* and *Graphina*, with many names antedating *Phaeographina* Müll. Arg., although the latter has been in general use since its publication. In the same way, a type species should be chosen and *Phaeographina* conserved without prejudice against older names, if the genus is divided.

Thallus crustose, epi- or endophloeodal, ecorticate or with a cortex of periclinal hyphae; algae *Trentepohlia*. Lirellae immersed to sessile, elongate or branched, lips connivent to open, entire or sulcate; parathecium entire or dimidiate, carbonaceous to hyaline; hypothecium thin, hyaline; paraphyses slender, unbranched; asci cylindric to somewhat rounded, 1–8-spored; ascospores muriform, brown, protoplasts rounded.

1. Disc pruinose 2
1. Disc not conspicuously pruinose 7
2. True parathecium absent, a pseudo-parathecium of bark cells and hyphae, forming dark brown lips, paler and thinner below; asci monosporous; ascospores 72 × 19 μ, 20-locular, 10-locellate; Sierra Leone ..... *P. innata* Dodge
2. True parathecium present 3
3. Asci monosporous; parathecium dark or black above, paler below 4
3. Asci 8-spored 5
4. Ascospores 45–90(–100) × 15–20 μ, 10–18-locular, 3–5-locellate; Usambara ..... *P. caesiopruinosa* f. *striolata* Zahlbr.
4. Ascospores 72–95 × 21–24 μ, 20-locular, 5–6-locellate; Sierra Leone ..... *P. Deightoni* Dodge
5. Parathecium wholly pale or brownish, not darker above 6
5. Parathecium dark fuscous, dimidiate; ascospores 42–48 μ long, 9–10-locular, (2)–3-locellate; lirellae subsessile, rounded to oblong, 0.7 mm. in diameter, cupulate, margin elevated, inflexed; Guinea ..... *P. pezizoidea* (Ach.) Müll. Arg.
6. Parathecium pale; ascospores 28–33 × 12–13 μ, 6-locular, 2–4-locellate; Mozambique ..... *P. mozambica* (Vainio) Zahlbr.
6. Parathecium pale brown; ascospores 29–32 × 12–13 μ, 8-locular, 3-locellate; Sierra Leone ..... *P. scriptitata* Dodge
6. Parathecium not described, probably pale; ascospores 50–75 × 18 μ; thallus hypophloeodal; São Thomé ..... *P. leucophora* (Nyl.) Dodge
7. Disc dark blood-red, lips open; ascospores 70–135 × 21–36 μ; thallus 70 μ thick; lirellae sessile, constricted at the base; São Thomé ..... *P. deducta* (Nyl.) Zahlbr.
7. Disc rufo-fuscous, lips connivent; ascospores 190 × 50–60 μ; thallus 2–5 mm. thick; lirellae immersed; Socotra ..... *P. Balfourii* Müll. Arg.
7. Disc not reddish 8

8. Lirellae immersed 9
8. Lirellae sessile 10
9. Ascospores 25–35 × 10 μ; thallus ashy olive, tuberculose, sorediose; Kenya ..... *Graphina sorediella* Müll. Arg.
9. Ascospores 110 × 26 μ; thallus dark fuscous, rimulose-areolate; Angola ..... *P. fuscescens* (Vainio) Zahlbr.
10. Parathecium entire, hyaline, subobsolete; ascospores 25–30 × 11–13 μ, 4–6-locular, 2-locellate; Kenya ..... *P. paucilocularis* Müll. Arg.
10. Parathecium dimidiate 11
11. Parathecium thin, not winged, dark brown; ascospores 45–50 × 15–18 μ, 10-locular, 5-locellate; Sierra Leone ..... *P. leptotremoides* Dodge
11. Parathecium thicker, winged at the base, carbonaceous; ascospores 170 × 30 μ, about 20-locular and 8-locellate; Sierra Leone ..... *P. alata* Dodge

Phaeographina **innata** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Anisophyllea laurina,* F. C. Deighton M4625.

Thallus obscure olivaceo-alutaceus, hypophloeodes, ad 40 μ crassitudine, cellulis suberosis emortuis, hyphis periclinalibus et filamentis *Trentepohliae* 4–5 μ diametro. Lirellae immersae, usque ad 4 × 0.7 mm., curvatae, rare furcatae, apertae, disco albido-pruinoso; pseudoparathecium cellulis suberosis hyphisque, labiis nigro-brunneis inferne brunneum; hypothecium 15 μ crassitudine, hyphis tenuibus dense contextum; thecium 110 μ altitudine, 375 μ latitudine; paraphyses tenues, semel vel bis dichotome ramosae, apicibus non incrassatis, crystallis minutis brunneis tectis; asci monospori, ellipsoidei juventute pachydermei, 80 × 24 μ; ascosporae brunneae, murales, 72 × 19 μ, saltem 20-loculares, 10-locellatae.

Thallus deep olive buff, mostly hypophloeodal, but forming a layer up to 40 μ thick, containing some disorganized bark cells, gelified, very slender, periclinal hyphae, and more or less disorganized filaments of *Trentepohlia* 4–5 μ in diameter. Lirellae immersed, up to 4 × 0.7 mm., curved, sometimes once-dichotomous, open, disc white-pruinose; no true parathecium but a pseudo-parathecium of bark cells separated by strands of hyphae, forming dark brown lips, 16–20 μ thick and 50 μ long, covering the margin of the thecium and sometimes represented by a brown line up to 8 μ thick under only a part of the hypothecium, otherwise indistinguishable from the rest of the bark cells; hypothecium 15 μ thick, of very slender, closely woven hyphae; thecium 110 μ tall, 375 μ broad; paraphyses slender, once or twice dichotomous, tips not thickened but partly covered by minute, brownish crystals in the brownish epithecial gel, 8–10 μ thick; asci monosporous, ellipsoid, 80 × 24 μ, thick-walled when young; ascospores brown, muriform, about 72 × 19 μ, at least 20-locular, 10-locellate.

The almost complete lack of parathecium and the dichotomous branching of the tips of the paraphyses are very unusual in *Phaeographina,* but the affinities of this species are clearly with this genus rather than with the Arthoniaceae (lack of parathecium) or with the Opegraphaceae (branched and anastomosing paraphyses forming a thick epithecium).

PHAEOGRAPHINA **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on branch of *Peltophorum africanum* v. *speciosum*, F. C. Deighton M4338.

Thallus epiphloeodes, 40–55 μ crassitudine, olivaceo-alutaceus; cortex 25–40 μ crassitudine, hyphis periclinalibus gelifactis, exteris brunneis; stratum algarum ca. 15 μ crassitudine, filamentis verticalibus *Trentepohliae* 6 μ diametro. Lirellae curvatae flexuosaeve, furcatae aut radiatim ramosae, 3–6 $\times$ 0.2–0.5 mm., labiis thallinis conniventibus, elevatis, mox delapsis, discum pruinosum exponentibus, thallo aequantem; parathecium 15 μ crassitudine, superne nigrum, inferne fulvum, integrum; hypothecium 10 μ crassitudine, hyphis tenuibus dense contextum; thecium 95 μ altitudine, 150 μ latitudine; paraphyses tenues; asci monospori, 70 $\times$ 18 μ, juventute pachydermei; ascosporae brunneae, murales, ellipsoideae, 20-loculares, 5–6-locellatae, 72–95 $\times$ 21–24 μ.

Thallus epiphloeodal, 40–55 μ thick, olive buff or darker depending on the color of the underlying bark; cortex 25–40 μ thick, of slender, gelified, periclinal hyphae, the outer 10 μ brownish; algal layer 15 μ thick, of vertical filaments of *Trentepohlia* about 6 μ in diameter; medulla not differentiated, the algal layer resting on the bark cells. Lirellae curved, flexuous, forked or radiately branched, 3–6 $\times$ 0.2–0.5 mm., covered by elevated, connivent thalline lips at first, which crack off exposing the pruinose disc level with the thallus; parathecium 15 μ thick, black above, fading to tawny in the lower half, entire; hypothecium 10 μ thick, of deeply staining, slender, densely woven hyphae; thecium 95 μ high, 150 μ wide; paraphyses slender, upper 10 μ slightly brownish; asci monosporous, 70 $\times$ 18 μ, thick-walled at first; ascospores brown, muriform, ellipsoid, about 20-locular and 5–6-locellate, 72–95 $\times$ 21–24 μ while still brown, shrinking to 55–69 $\times$ 15 μ, and subfusiform when very dark brown.

PHAEOGRAPHINA **leucophora** Dodge, comb. nov.
Lecanactis leucophora Nyl., Flora 69:176. 1886.

PHAEOGRAPHINA **scriptitata** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on branches of *Citrus aurantifolia*. F. C. Deighton M4628.

Thallus epiphloeodes, 90–100 μ crassitudine, cartilagineus, alutaceo-olivaceus; cortex 40–50 μ crassitudine, gelifactus, hyphis periclinalibus septatis 3 μ diametro, strato algarum discontinuo usque ad 30 μ crassitudine, cellulis *Trentepohliae?* 10–11 μ diametro tectus; stratum algarum verum 40 μ crassitudine, filamentis verticalibus *Trentepohliae* 6–8 μ diametro. Lirellae elongatae flexuosaeque, 5 $\times$ 0.5 mm. aut ramosae, subdendroideae, immersae aut subimmersae, disco subconcavo, caesio-pruinoso, madefacto livido, siccitate thecio ab labiis circumscisso; parathecium 55 μ crassitudine, integrum, pallide brunneum; hypothecium vix evolutum; thecium 120 μ altitudine; paraphyses tenues, apicibus non incrassatis, granulis brunneis tectis; asci ellipsoidei aut fusiformes, stipite 15 μ longitudine,

115 × 22 μ; ascosporae octonae, imbricatim distichae, brunneae, murales, ellipsoideae, 8-loculares, 3-locellatae, protoplastis rotundatis, 29–32 × 12–13 μ.

Thallus epiphloeodal, 90–100 μ thick, cartilaginous, buffy olive; cortex 40–50 μ thick, gelified, of periclinal, septate hyphae about 3 μ in diameter, covered by a discontinuous algal layer of variable thickness, up to 30 μ thick, of disorganized *Trentepohlia* filaments 10–11 μ in diameter; true algal layer 40 μ thick, of vertical filaments of *Trentepohlia* 6–8 μ in diameter, resting on the bark cells, with occasional filaments penetrating much deeper into the bark. Lirellae immersed or very slightly elevated, long-flexuous, 5 × 0.5 mm., or variously branched, subdendroid, closely aggregated, disc soon exposed, slightly concave and densely chalky-pruinose, livid when moistened, thecium tending to crack away from the lips when dry; parathecium 55 μ thick, entire, pale brownish; hypothecium scarcely differentiated; thecium 120 μ tall; paraphyses slender, tips not thickened, covered with brownish granules in the upper 10 μ; asci 8-spored, ellipsoid to fusiform, stipe about 15 μ long, 115 × 22 μ; ascospores imbricately monostichous, brown, muriform, ellipsoid, mostly 8-locular, 3-locellate, protoplasts rounded, sometimes slightly constricted at the septa when mature, 29–32 × 12–13 μ.

The interpretation of this species is difficult. If the outer algal layer represents purely epiphytic growths, it is strange that the algae should be so uniform. The cells are larger and the walls thicker than those of the *Trentepohlia* filaments in the true algal layer, but they have the usual color of *Trentepohlia*. There are also somewhat irregular blackened masses in the parathecium and rarely also below the thecium, but they are apparently adventitious in contrast to the regularly darkened upper portion of the parathecium in *P. caesiopruinosa*. *P. scriptitata* seems closest to *P. mozambica* (Vainio) Zahlbr., from which it differs in its somewhat darker thallus, shorter, more curved and branched lirellae, more brownish parathecium which does not extend above the thecium, much broader disc, and its more septate spores.

Phaeographina deducta Zahlbr., Cat. Lich. Univ. 2:437. 1923.

Lecanactis Montagnei subsp. *deducta* Nyl., Flora 69:176. 1886.
Lecanactis Montagnei subsp. *deducens* Nyl., Lich. Insul Guineens. 32. 1889 (*lapsus calami?*, repeating the description verbatim).
Graphis deducta Vainio, Cat. Welwitsch Afric. Pl. 2:436. 1901.

Type: *Lecanactis Montagnei* subsp. *deducta* Nyl. was based on São Thomé, Rodia, 550 m., Monte Cafe, Saudade, 700 m., A. Moller, comm. J. Henriques, and subsp. *deducens* Nyl. on São Thomé, 550–700 m., corticole, Moller.

Thallus epiphloeodal, 70 μ thick, olivaceus black; cortex 30 μ thick, of highly gelified periclinal hyphae; algal layer 40 μ thick, of rather disorganized, vertical filaments of *Trentepohlia* 5–8 μ in diameter, tending to die off below, leaving lacunae between the hyphae but no medulla differentiated. Lirellae circular, about 1 mm. in diameter, to elongate, flexuous or lobulate, very rarely branched, 5–6 × 1 mm., elevated and somewhat constricted at the base; amphithecium prominent,

slightly inflexed, lips spreading, disc open, not pruinose, claret brown; parathecium entire, carbonaceous, about 100 μ thick above to 125–150 μ thick at the angled base, vertical or slightly spreading, 125 μ thick below the hypothecium which is scarcely differentiated; thecium 135 μ tall; paraphyses slender with abundant oil droplets, with flexuous, deeply staining hyphae about 3 μ in diameter (resembling latex vessels of the Autobasidiomycetes) which apparently produce the amorphous red covering of the thecium; asci clavate with stipes 15 μ long, thick-walled and 4-spored when young, only maturing a single spore; ascospores brown, muriform, 24-locular, 5-locellate, 80–100 $\times$ 22 μ.

Probably Nylander had only a portion of a thallus with the circular lirellae, when superficially it would look like a large *Haematomma*, while its microscopic structures would place it in his *Lecanactis*, since Nylander seldom used spore septation as a generic character.

After the ascospores are shed, the thecium quickly begins to disintegrate and is covered by thalline cortex and eventually some thalline algae. Later a new lirella forms on the base of the old parathecium. In contrast to most Graphidaceae where this occurs, only a part of the old parathecium is occupied, so that we may have 3–4 new lirellae along an old one, sometimes with the long axis parallel to that of the old one, sometimes nearly transverse.

Fernando Po Island: Izaguirre estate near Botonos, 550 m., on *Theobroma*, C. A. Thorold 167.

PHAEOGRAPHINA **leptotremoides** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on bark of *Bauhinia tomentosa*, F. C. Deighton M4307.

Thallus epiphloeodes, superficie laevi, opaca, albidus, 40 μ crassitudine; cortex 10 μ crassitudine, hyphis periclinalibus gelifactis; stratum algarum 30 μ crassitudine, filamentis periclinalibus *Trentepohliae* 5–6 μ diametro; medulla non bene evoluta, vicinitate parathecii excepta ubi hyphae tenues crystallos magnos includunt, ut in *Leptotremate*. Lirellae emersae, usque ad 2.5 $\times$ 0.3 mm., basi subconstrictae, labiis conniventibus, ter profunde sulcatae, nigrae, rectae vel curvatae, rare furcatae; parathecium dimidiatum, ad labias 15 μ crassitudine, in lateribus ad 20 μ dilatatum, obscure brunneum, hyphis periclinalibus; hypothecium 8 μ crassitudine; thecium cordiforme, 60 μ altitudine latitudineque; paraphyses tenues, apicibus non incrassatis; asci ellipsoidei; ascosporae brunneae, muriformes, ca. 10-loculares, 5-locellatae, probabiliter 45–50 $\times$ 15–18 μ, nunc collapsae, 30 $\times$ 11 μ.

Thallus epiphloeodal, surface smooth, dull whitish, 40 μ thick; cortex 10 μ thick, of gelified, periclinal hyphae 5–6 μ in diameter; algal layer 30 μ thick, of periclinal filaments of *Trentepohlia* 5–6 μ in diameter, medulla not differentiated except in the vicinity of the parathecium where the hyphae enclose very large crystals as in *Leptotrema*. Lirellae emersed, up to 2.5 $\times$ 0.3 mm., somewhat constricted at the base, lips connivent, up to thrice deeply sulcate, black, straight or curved, sometimes once dichotomous; parathecium dimidiate, 15 μ thick at the lips, expanding to 20 μ on the sides, very dark brown, of periclinal hyphae; hypothecium about 8 μ thick, resting on the bark cells; thecium cordate, 60 μ tall and

broad; paraphyses slender, tips not thickened; asci monosporous?, ellipsoid; ascospores muriform, brown, at least 10-locular, 5-locellate, probably 45–50 × 15–18 μ, shrinking to 30 × 11 μ.

The youngest lirella sectioned has the sides covered with the thallus; the parathecium has lips up to 30 μ thick, expanding to 55 μ on the sides, with the uppermost bark cells darkened; the thecium is only 45 μ tall and 80 μ broad; the paraphyses are attached at both top and bottom; no asci seen. After the first thecium has disintegrated, a new thecium forms from the old hypothecium and new parathecial walls grow out of the lower inner margins of the old parathecium, spreading the old parathecial lips, leaving a curving space about 20 μ wide extending about halfway down the old parathecium, filled with the gelified remains of the old thecium. This process may be repeated, leaving at least three incurved lips. Sometimes the outermost lips break off and the thallus covers the broken stumps.

The Cameroons lirella sectioned is still in the one-lipped stage, but the thecium has nearly disintegrated. A single brown shrunken ascospore was found in these sections, and one in the old thecium of an early 2-lipped stage from the Sierra Leone material. Probably before the spores shrank, they measured about 45–50 × 15–18 μ, judging from my experience with other species where both mature and shrunken ascospores have been found in the same thecium.

Sierra Leone: Njala (Kori), on bark of *Bauhinia tomentosa,* F. C. Deighton M4307.

Cameroons: Tombel, on *Theobroma,* C. A. Thorold 125.

PHAEOGRAPHINA **alata** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Peltophorum africanum* v. *speciosum,* F. C. Deighton M4339.

Thallus epiphloeodes, 40 μ crassitudine, alutaceo-brunneus; ecorticatus; cellulis *Trentepohliae* 7 μ diametro, subellipsoideis; medulla hyphis tenuibus, verticalibus dense contexta. Lirellae emersae, simplices, rare curvatae vel furcatae, 300 μ altitudine, 1–2 × 0.5 mm., dimidiatae, labiis conniventibus; parathecium superne 75 μ crassitudine ad 180 μ in lateribus basique alata usque ad 330 μ dilatatum, carbonaceum, partim strato thalliño tenui tectum; hypothecium 6–8 μ crassitudine, hyphis tenuibus dense contextum in strato cellularum suberosarum brunnearum 25 μ crassitudine impositum; thecium rotundatum, 300 μ altitudine, 360 μ latitudine; paraphyses tenues, apicibus non incrassatis, guttulis oleosis superne inspersae; asci clavati dein ellipsoidei, 180 × 32 μ pachydermei, monospori; ascosporae brunneae, muriformes, ad 20-loculares, dein quoque loculo diviso et cellulis irregulariter dispositis, 175 × 30 μ.

Thallus epiphloeodal, 40 μ thick, between buffy brown and citrine drab; ecorticate; cells of *Trentepohlia* about 7 μ in diameter, somewhat ellipsoid, irregularly arranged in the upper part of the thallus; medulla of densely woven, predominantly vertical hyphae. Lirellae emersed, 300 μ tall, 1–2 × 0.5 mm.,

dimidiate, lips connivent, simple, rarely somewhat curved or forked; parathecium 75 μ thick above, expanding to 180 μ on the sides and extending 330 μ beyond the thecium at the base, carbonaceous, covered on the lower two thirds by a thin decomposed layer of thallus; hypothecium 6–8 μ thick, of densely woven, deeply staining, slender hyphae resting on a layer of bark cells about 25 μ thick, deeper brown than those below; thecium rounded, 300 μ tall, 360 μ broad; paraphyses slender, unbranched, tips not thickened, with oil droplets in the upper portion of the thecium; asci monosporous, clavate at first, walls 5 μ thick, becoming ellipsoid and thin-walled, 180 $\times$ 32 μ; ascospores brown, muriform, about 20-locular at first, then each locule is further divided by septa in all three planes and the protoplasts become quite irregularly arranged, 175 $\times$ 30 μ.

In thick sections, the dark brown bark cells may be mistaken for the base of the parathecium which would then appear entire instead of dimidiate.

Chiodectonaceae

Thallus crustose, homoeomerous or heteromerous, hypothallus often slightly developed, ecorticate or with a slight, almost amorphous cortex; algae *Trentepohlia* or *Phycopeltis*. Lirellae in stromata usually immersed, rounded or elongate, simple or branched; parathecium black or hyaline; paraphyses simple or branched and anastomosing; ascospores septate or muriform, protoplasts cylindric or rounded; spermatia exobasidial.

The family as now constituted included all the stromatic lichens related to the Opegraphaceae and Graphidaceae. Here we have the same problems we have in the relationships of the Pyrenulaceae and Trypetheliaceae, although there are not so many intermediate species. *Ptychographa* Nyl. and *Diplogramma* Müll. Arg. perhaps should belong with this family as they have 2–4 parallel thecia immersed in a sort of stroma. The stroma with its immersed lirella is often called a sarcothecium.

1. Corticole, rarely saxicole, with *Trentepohlia* algae 2
1. Foliicole, with *Phycopeltis* algae 10
   2. Paraphyses simple, free 3
   2. Paraphyses branched and anastomosing 7
3. Ascospores with rounded to lenticular protoplasts 4
3. Ascospores with cylindric protoplasts and thin septa; muriform ..... *Enterodictyon* Müll. Arg.
   4. Ascospores septate 5
   4. Ascospores muriform 6
5. Ascospores hyaline ..... *Glyphis* Ach.
5. Ascospores brown ..... *Sarcographa* Fée
   6. Ascospores hyaline ..... *Medusulina* Müll. Arg.
   6. Ascospores brown ..... *Sarcographina* Müll. Arg.
7. Ascospores septate 8
7. Ascospores muriform 9
   8. Ascospores hyaline ..... *Chiodecton* Ach.
   8. Ascospores brown ..... *Sclerophyton* Eschw.
9. Ascospores hyaline ..... *Minksia* Müll. Arg.
9. Ascospores brown ..... *Enterostigma* Müll. Arg.
   10. Paraphyses unbranched and free ..... *Pycnographa* Müll. Arg.
   10. Paraphyses branched and anastomosing ..... *Mazosia* Mass.

GLYPHIS

GLYPHIS Ach., Syn. Lich. 107. 1814.

Graphis subg. *Scolaecospora* sect. *Glyphis* Vainio, Etude Lich. Brésil 2:127. 1890.

Type: not designated. *G. cicatricosa* Ach. may be chosen to conserve the name in its present use, as *G. labyrinthica* and *G. tricosa* have been transferred to *Sarcographa.*

Thallus crustose, epi- or endophloeodal, ecorticate or with an almost amorphous cortex of periclinal hyphae; algae *Trentepohlia.* Lirellae immersed to subsessile on a black stroma, elongate, branched or somewhat rounded; parathecium black with entire lips, disc flat; hypothecium hyaline; paraphyses unbranched, free; asci clavate with thickened tips, 4–8-spored; ascospores ellipsoid to fusiform, septate, with lenticular protoplasts, hyaline.

Ascospores 27–30 × 8 μ, 8-locular; sarcothecia 3 mm. in diameter; Guinea.....*G. cicatrosa* Ach.
Ascospores 40–52 × 10 μ, 8–10-locular; sarcothecia up to 8 × 5.5 mm.; Mozambique.....
.....*G. latissima* (Vainio) Zahlbr.

GLYPHIS CICATRICOSA Ach., Syn. Lich. 107. 1814.

Graphis cicatricosa Vainio, Etude Lich. Brésil 2:127. 1890.

Type: Guinea, on *Cordaria acutifolia* Afz. (*Dialia guineensis* Willd.) Afzelius.

Thallus mostly hypophloeodal, buffy brown, black-margined, at least next the thalli of other lichens; cortex gelified, about 25 μ thick, of periclinal hyphae; filaments of *Trentepohlia,* 5–6 μ in diameter, mostly between the bark cells. Sarcothecia circular, subcrenate, up to 3 mm. in diameter in our material, margin ashy, narrow, very slightly elevated, lirellae radiately dendroid-branched and lobulate, disc flat to slightly concave, brown, lips thin, spreading, black; stroma carbonaceous, about 115 μ thick; in the younger portions cortex of vertical brownish hyphae covered with minute granules which disappear in the older portions; parathecium about 15 μ thick, usually concrescent with the stroma in the older portions; hypothecium about 15 μ thick, of densely woven, deeply staining hyphae; thecium 80 μ tall; paraphyses slender, tips pyriform and brownish, about 8 × 3 μ; asci clavate, 8-spored, thick-walled when young, about 67 × 19 μ; ascospores imbricately monostichous, somewhat twisted, hyaline, fusiform, thick-walled, 8-locular, protoplasts rounded, 27–30 × 8 μ.

Sierra Leone: Njala (Kori), on *Bauhinia tomentosa,* F. C. Deighton M4307D; M4307G.

Var. **pulvinata** Dodge, var. nov.

Type: Sierra Leone, Njala (Kori), on *Peltophorum africanum* var. *speciosum,* F. C. Deighton M4343.

Thallus epiphloeodes, 65 μ crassitudine, olivaceo-brunneus; cortex 25 μ crassitudine, hyphis tenuibus periclinalibus gelifactis; stratum algarum 40 μ crassitudine, filamentis verticalibus *Trentepohliae;* sarcothecia pulvinata, basi subconstricta,

orbicularia, 1–1.5 mm. diametro, 0.33 mm. altitudine; stroma 220–250 μ crassitudine sub theciis; parathecium 8 μ crassitudine; ascosporae 8-loculares, uno apice obtuso, altero acuto, 32 × 8 μ.

Thallus 65 μ thick, epiphloeodal, olive brown; cortex 25 μ thick, of gelified, periclinal, slender hyphae; algal layer 40 μ thick, of subvertical filaments of *Trentepohlia* above the bark cells; sarcothecia pulvinate, slightly constricted at the base, circular, 1–1.5 mm. in diameter, 0.33 mm. tall; stroma 220–250 μ thick below the thecia; parathecium 8 μ thick; ascospores 8-locular, one end obtuse, the other acute, 32 × 8 μ.

SARCOGRAPHA

SARCOGRAPHA Fée, Essai Crypt. Ecorces Officin. xxxv, 38. 1824.

Asterisca Meyer, Nebenstudien, 331. 1825.
Actinoglyphis Mont., Syll. Gen. Sp. Crypt. 355. 1856.

Type: not designated; *S. Cascarillae, S. Cinchonarum* and *S. tigrina* were described. *Asterisca* Meyer was based on *Glyphis labyrinthica* Ach. and *G. tricosa* Ach. *Actinoglyphis* Mont. was based on *A. Leprieurii* Mont.

Thallus crustose, epi- or endophloeodal, ecorticate or with an almost amorphous cortex of periclinal hyphae; algae *Trentepohlia.* Sarcothecia carbonaceous in sect. *Eusarcographa* or hyaline in sect. *Phaeoglyphis;* parathecium well developed and carbonaceous to rudimentary; lirellae usually branched; paraphyses unbranched, free; asci clavate with thickened tips; ascospores brown, septate with lenticular protoplasts.

Stroma dark brown; parathecium carbonaceous; ascospores 14–20 × 6–8 μ, 4–6 (–8)-locular; Guinea ..... *S. labyrinthica* (Ach.) Müll. Arg.
Stroma pale brownish; parathecium pale; ascospores 18–19 × 5–6 μ, 4-locular; Fernando Po ..... *S. Thoroldi* Dodge

SARCOGRAPHA LABYRINTHICA Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 29:8:62. 1887.

Glyphis labyrinthica Ach., Syn. Lich. 107. 1814.
Asterisca labyrinthica Meyer, Nebenstudien, 161. 1825.
Graphis labyrinthica Vainio, Cat. Welwitsch Afric. Pl. 2:439. 1901.

Type: Guinea, corticole, Afzelius.

Thallus epiphloeodal, about 80 μ thick, deep olive buff to citrine drab; cortex 40 μ thick, gelified, of densely woven, mostly periclinal hyphae; algal layer 40 μ thick, of somewhat disorganized, vertical filaments of *Trentepohlia* 5–6 μ in diameter. Sarcothecia rounded, up to 4 mm. in diameter, then coalesced into much larger, irregular areas, white-pruinose; lirellae labyrinthiform, very narrow, open, disc pruinose, the thecium shrinking and cracking away from one side of the parathecium when dry, giving the appearance of minute, partly connivent lips, but the disc level with the top of the parathecium when moist and no cracks visible; parathecium entire, fuscous above, dark fuscous to carbonaceous below,

8 μ thick above to 15 μ below, immersed in the stroma of lighter brown pseudoparenchyma; hypothecium not well differentiated, of closely packed, vertical septate hyphae, somewhat more deeply staining in the lower 25 μ of the thecium; thecium 100 μ tall; paraphyses slender, tips thickened and brown in the upper 8 μ; asci cylindric-clavate, thick-walled when young, 60 $\times$ 12–13 μ, 8-spored; ascospores imbricately monostichous to subdistichous, oblong-ellipsoid, brownish, 4–6(–8)-locular, protoplasts rounded, 14–20 $\times$ 6–8 μ.

Sierra Leone: Njala (Kori), on *Peltophorum africanum* v. *speciosum*, F. C. Deighton M4336, on *Anisophyllea laurina*, F. C. Deighton M4403, and on *Citrus aurantifolia*, F. C. Deighton M4424, M4626.

Nigeria: Ehor near Benin City, on *Theobroma*, C. A. Thorold 123.

Cameroons: Tombel, on *Theobroma*, C. A. Thorold 122, 136.

Sarcographa (Phaeoglyphis) **Thoroldi** Dodge, sp. nov.

Type: Fernando Po, Izaguirre estate, 550 m., near Botonos, on *Theobroma*, C. A. Thorold 166.

Thallus epiphloeodes, 70–80 μ crassitudine, obscure olivaceo-griseus; cortex gelifactus, 15 μ crassitudine, hyphis periclinalibus; stratum algarum 55–65 μ crassitudine, filamentis *Trentepohliae* subverticalibus laxe dispositis, 4–5 μ diametro. Sarcothecia rotundata, usque ad 5 mm. diametro, in gregibus irregularibus confluentia, 2.5 $\times$ 1 cm.; stroma pallide brunnea, 130–160 μ crassitudine; parathecium superne 20 μ crassitudine, inferne ad 40 μ dilatatum, pseudoparenchymate leptodermeo, sub hypothecio 20 μ crassitudine, hyphis periclinalibus pallide brunneis; hypothecium 25 μ crassitudine, hyphis subverticalibus dense contextum; thecium 95 μ altitudine; paraphyses tenues, apicibus incrassatis brunneis, epithecium 8 μ crassitudine formantes; asci juventute pachydermei, cylindrico-clavati, 65 $\times$ 8 μ; ascosporae octonae, submonostichae, brunneae, oblongae, 4-loculares, protoplastis rotundatis, 18–19 $\times$ 5–6 μ.

Thallus epiphloeodal, 70–80 μ thick, dark grayish olive; cortex 15 μ thick, gelified, of periclinal hyphae; algal layer 55–65 μ thick, of loosely arranged, subvertical filaments of *Trentepohlia* 4–5 μ in diameter, some filaments penetrating deeper between the bark cells. Sarcothecia rounded, up to 5 mm. in diameter, confluent into irregular areas up to 2.5 $\times$ 1 cm., stroma pale brownish, about 130–160 μ thick; parathecium 20 μ thick above to 40 μ below, of thin-walled pseudoparenchyma, 20 μ thick below the hypothecium, of periclinal light brown hyphae; hypothecium 25 μ thick, of densely woven, deeply staining, subvertical hyphae; thecium 95 μ tall; paraphyses slender, tips slightly enlarged and brownish, forming an epithecium 8 μ thick; asci thick-walled when young, 8-spored, cylindric-clavate, 65 $\times$ 8 μ; ascospores submonostichous, brownish, oblong, 4-locular, protoplasts rounded, 18–19 $\times$ 5–6 μ.

CHIODECTON

CHIODECTON Ach., Syn. Lich. 108. 1814.

Hypochnus Ehrenb. in Nees, Horae Phys. Berol. 84. 1820, *non* Fr. 1818.
Syncesia Tayl. in Mackay, Fl. Hibern. 2:103. 1836.
Melanodecton Mass., Atti I. R. Ist. Veneto III, 5:324. 1860.

Type: not designated. *C. sphaerale* and *C. seriale* described, both in subg. *Euchiodecton*. *Hypochnus* Ehrenb. was based on *H. rubrocinctus* Ehrenb., a synonym of *C. sanguineum* (Sw.) Vainio in subg. *Byssophorum*. *Syncesia* was based on *S. albida* Taylor, usually included in subg. *Euchiodecton*. *Melanodecton* Mass. was based on *Chiodecton sphaerale* Ach. and *M. indicum* Mass. Since the subgenus *Enterographa* (Fée) Müll. Arg. with hyaline stromata and parathecia is often recognized as a separate genus, I have not included its synonymy here, as none of the names would displace those listed above if the genus were to be divided.

Thallus epiphloeodal (sometimes epilithic in subg. *Enterographa*); ecorticate; algae *Trentepohlia*. Sarcothecia with immersed or sessile lirellae which may be rounded or elongate; parathecium carbonaceous, well developed, greatly thickened below to thin and rudimentary above, hyaline below (in subg. *Enterographa*); paraphyses branched and anastomosing; ascospores fusiform to acicular, hyaline, septate with cylindric protoplasts.

1. True stromata without algae; the bases of parathecia very thick, usually confluent below; subg. EUCHIODECTON 2
1. Pseudostromata with algae, containing several thecia; often sterile; thallus of very loosely woven hyphae and filaments of *Trentepohlia*, margin byssoid, wide, usually of a different color from the rest of the thallus; subg. BYSSOPHORUM 10
2. Ascospores 4-locular 3
2. Ascospores 4–6-locular, 22–35 μ long; disc 0.8–1.3 mm., pruinose; sarcothecia poorly developed; Mozambique ..... *C. rotundatum* Vainio
2. Ascospores 6–8-locular 8
2. Ascospores 10–12-locular 9
3. Ascospores more than 5.5 μ broad; thallus white 4
3. Ascospores not over 4 μ broad 5
4. Ascospores 23–26 × 5.5–6.5 μ; Socotra ..... *C. socotranum* Müll. Arg.
4. Ascospores 30–35 × 6–7 μ; Mozambique ..... *C. amyloplacoides* Vainio
5. Ascospores 26–30 × 3–4 μ 6
5. Ascospores 39–44 × 3–4 μ; sarcothecia 1–2.5 × 0.8–1.5 mm., disc blackening; Mozambique ..... *C. palmensis* Vainio
6. Thallus with loose byssine margin; sarcothecia 2.5–4 × 0.9–1.5 mm., disc ashy-pruinose; Mozambique ..... *C. laceratum* Vainio
6. Thallus margin inconspicuous or partly dark 7
7. Sarcothecia circular to oblong, 1 mm. broad; disc 50–100 μ in diameter; ascospores 26–30 × 3–4 μ; Kenya ..... *C. minutulum* Müll. Arg.
7. Sarcothecia oblong to irregular, 0.8–2 × 0.8–1.5 mm.; ascospores 30 × 2–4 μ; Mozambique ..... *C. mozambicum* Vainio
8. Ascospores 21–24 × 5 μ; disc 20–50 μ in diameter; sarcothecia 0.2 mm.; Socotra ..... *C. nanum* Müll. Arg.
8. Ascospores 28–44 × 3–4 μ; disc 80–100 μ; sarcothecia 0.4–2 mm.; Kenya ..... *C. irregulare* Zahlbr.
9. Ascospores 36 × 5 μ; disc 160–250 μ; Socotra ..... *C. circumscissum* Müll. Arg.
9. Ascospores 34–40 × 2.5–4 μ; disc 300–600 μ; Angola ..... *C. amyloplacum* Vainio
10. Thallus white; sterile 11
10. Thallus glaucous or yellowish; fertile 12

11. Thallus easily separating from the substrate, white above, yellow below, margin somewhat tawny; Usambara ..... *C. hypochryseum* Müll. Arg.
11. Thallus not easily separating, covered with white isidioid soredia, white below, margin white; Sierra Leone ..... *C. album* Dodge
12. Ascospores 4-locular, 45–50 × 4.5–5 μ 13
12. Ascospores 8-locular, 70–80 × 3.5–4 μ; thallus glaucescent, black below, surface isidiose; many minute rounded lirellae per sarcothecium; Usambara ..... *C. Brunnthaleri* Zahlbr.
13. Thallus thin, pale green to ashy; lirellae forked or branched, many per sarcothecium; Usambara ..... *C. intercedens* Müll. Arg.
13. Thallus thick, pale yellow; lirellae rounded, few per sarcothecium; Usambara.... *C. molle* Müll. Arg.

Chiodecton (Byssophorum) **album** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on trunk of *Phyllanthus discoideus*, F. C. Deighton M4396.

Thallus albus, byssinus, margine radiato-fibrilloso, minutis sorediis isidioideis tectus, 25–50 μ crassitudine; ecorticatus; filamentis *Trentepohliae* 11 μ diametro, cellulis 15 μ longitudine et hyphis tenuibus ramosis laxe intertextis cum crystallis usque ad 3 μ diametro. Sterilis.

Thallus white, byssine, margin radiately fibrillose, covered with minute white isidioid soredia, 25–50 μ thick; ecorticate; filaments of *Trentepohlia* mostly between the bark cells with an occasional branch pushing up through the thallus and forming the soredia, about 11 μ in diameter, cells 15 μ long; the rest of the thallus of slender, branched and intricately but loosely tangled hyphae 1.5 μ in diameter, enclosing abundant hyaline crystals up to 3 μ in diameter. Sterile.

The habit is similar to *Chiodecton (Byssophorum) sanguineum* (Sw.) Vainio, but rather thinner, more sorediose and containing hyaline instead of red crystals. As it is sterile, the systematic position of this species is uncertain, since sometimes Cryptotheciaceae have somewhat similar thalli but usually are more closely woven and clearer differentiation of algal layer and medulla.

Lecanactidaceae

Thallus crustose, attached to the substrate by hyphae of the medulla; ecorticate; algae *Trentepohlia*. Apothecia round or nearly so, innate or sessile; amphithecium present or absent; parathecium well developed or rudimentary; paraphyses branched and anastomosing; asci 8-spored; ascospores unilocular, septate or dwarf-muriform.

Although placed in the Cyclocarpineae by Zahlbruckner, this family shows much closer relationships with the Arthoniaceae and Opegraphaceae, differing from the former by the presence of at least a rudimentary parathecium and from the latter by more-rounded apothecia.

1. Parathecium well developed, entire; ascospores hyaline 2
1. Parathecium rudimentary 3
2. Ascospores unilocular ..... *Pseudolecanactis* Zahlbr.
2. Ascospores bilocular, ellipsoidal ..... *Catinaria* Vainio
2. Ascospores 4–16-locular, fusiform to acicular ..... *Lecanactis* Eschw.
3. Amphithecium present; ascospores septate ..... *Schismatomma* Mass.
3. Amphithecium absent; ascospores septate or dwarf muriform ..... *Melampidium* Stirton

LECANACTIS

LECANACTIS Eschw., Syst. Lich. 14. 1824; Fries, Syst. Orb. Veg. 274. 1825.

Type: based on *Opegrapha astroidea* Smith & Sow., *non* Ach., and *Lichen lynceus* Smith & Sow. Eschweiler also figures *L. lobata* Eschw. None of these species are now included in *Lecanactis*, as their apothecia are elongate. Fries added *Opegrapha illecebrosa* Duf., which now is considered a synonym of *L. amylacea* (Ehrh.) Arn. Hence Fries' usage, based on *Opegrapha illecebrosa* Duf., should be conserved.

Thallus crustose, mostly homoeomerous, attached to the substrate by medullary hyphae; algae *Trentepohlia*. Apothecia innate to sessile, round, with black, thin parathecium; paraphyses branched and anastomosing, forming a thick epithecium; asci 8-spored; ascospores fusiform to acicular, septate, protoplasts cylindric. Spermogonia spherical, upper half of wall dark; spermatia exobasidial, ellipsoid to cylindric.

1. Disc black; ascospores 17–21(–24) × 3.5 μ, (4–)6–8-locular; apothecia 1 mm. in diameter; Sierra Leone ..... *L. Deightoni* Dodge
1. Disc yellow-pruinose 2
   2. Ascospores 20–26 × 4–6 μ, 7–10-locular; apothecia 0.6–1 mm. in diameter; Mozambique ..... *L. flavescens* Vainio
   2. Ascospores 15–16 × 4–5 μ, 4-locular; apothecia 0.4–0.6 mm. in diameter; Angola ..... *L. flava* Vainio

LECANACTIS **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Cathormion Dinklagei*, F. C. Deighton M3734.

Thallus hypophloeodes, cortex 18–20 μ crassitudine, hyphis tenuibus conglutinatis; stratum algarum 10–15 μ crassitudine super cellulas suberosas, filamentis *Trentepohliae* 5–6 μ diametro, corticem arboris penetrantibus usque ad 140 μ. Apothecia sessilia, basi constricta, rotundata, 1 mm. diametro aut greges ad 3 mm. diametro formantia, margine sicco prominente, nigro; parathecium integrum, 15 μ sub hypothecio superne ad 40 μ, hyphis nigro-brunneis, pachydermeis, periclinalibus; hypothecium subbrunneum, 8 μ crassitudine, hyphis periclinalibus 2 μ diametro; thecium 80 μ altitudine; paraphyses sparsae, tenuissimae, superne dense ramosae anastomosantesque, epithecium nigro-brunneum formantes; asci clavati, 56 × 10 μ; ascosporae octonae, ellipsoideae, rectae vel subcurvatae, (4–)6–8-loculares, protoplastis cylindricis, 17–21(–24) × 3.5 μ.

Thallus mostly hypophloeodal, cortex 18–20 μ thick, of slender, conglutinate hyphae; algal layer 10–15 μ thick above the bark cells, filaments of *Trentepohlia* 5–6 μ in diameter, rather disorganized but penetrating the bark 140 μ deep, separating layers of bark cells and forming cavities filled with contorted filaments. Apothecia sessile, constricted at the base, round, 1 mm. in diameter or forming groups up to 3 mm. in diameter, then distorted by mutual pressure but not coalescent, margin slightly prominent when dry, black both wet and dry; parathecium entire, 15 μ thick below the hypothecium expanding to 40 μ thick around the thecium, of very dark brown, periclinal, thick-walled hyphae; hypothecium

about 8 μ thick, of periclinal, pale brown hyphae about 2 μ in diameter; thecium 80 μ tall; paraphyses sparse, very slender, densely branched and anastomosing above to form the dark brown epithecium 20 μ thick, thecial gel I blue; asci clavate, 8-spored, 56 $\times$ 10 μ; ascospores hyaline, long-ellipsoid, straight or slightly curved, (4–)6–8-locular, walls and septa very thin, protoplasts cylindric, 17–21(–24) $\times$ 3.5 μ.

Thelotremaceae

Thallus crustose, ecorticate or with a more or less amorphous cortex; with *Trentepohlia* or *Phyllactidium* algae, usually with a loosely woven medulla, enclosing large hyaline crystals. Apothecia usually immersed in thalline warts or partly emersed, or several united into a pseudostroma *(Tremotylium)* or proliferating from the margin to form rows of apothecia *(Polystroma)*; amphithecium and parathecium well developed, usually partly covering the thecium and opening by a wide ostiole; thecium entire or pierced by a central columella; paraphyses usually simple and free, rarely branched and anastomosing *(Gyrostomum)*; asci 1–8-spored; ascospores septate or muriform, hyaline or brown.

1. Apothecia proliferating from the margin of the older apothecia, forming more or less erect, forked chains of apothecia.....*Polystroma* Clemente
1. Apothecia united into stromata; paraphyses branched and anastomosing; ascospores muriform, hyaline or brown.....*Tremotylium* Nyl.
1. Apothecia single or somewhat aggregated, but not united into stromata.....2
   2. Corticolous, very rarely saxicolous; algae *Trentepohlia*.....3
   2. Foliicolous; algae *Phyllactidium;* ascospores hyaline.....7
3. Paraphyses branched and anastomosing.....*Gyrostomum* Fr.
3. Paraphyses unbranched.....4
   4. Ascospores septate.....5
   4. Ascospores muriform.....6
5. Ascospores hyaline.....*Ocellularia* Meyer
5. Ascospores brown.....*Phaeotrema* Müll. Arg.
   6. Ascospores hyaline.....*Thelotrema* Ach.
   6. Ascospores brown.....*Leptotrema* Mont. & v. d. Bosch
7. Ascospores septate.....*Phyllophthalmaria* Zahlbr.
7. Ascospores muriform.....*Chroodiscus* Müll. Arg.

TREMOTYLIUM

TREMOTYLIUM Nyl., Bull. Soc. Linn. Normandie II, 2:513. 1868.

Type: *T. angolense* Nyl.

Thallus crustose, ecorticate or with an amorphous cortex; algae *Trentepohlia.* Apothecia crowded, forming pseudostromata, each apothecium with its own well-developed parathecium; paraphyses branched and anastomosing; asci 1–8-spored; ascospores hyaline (brown in *T. occultum* Stirton), muriform, protoplasts rounded.

Thallus white; asci 2–8-spored; ascospores 95–170 $\times$ 23–46 μ; Angola.....*T. angolense* Nyl.
Thallus pale ochre; asci 1–3-spored; ascospores 120–160 $\times$ 24–30 μ; Cameroons....*T. africanum* Räs.

TREMOTYLIUM AFRICANUM Räs., Arch. Soc. Zool. Bot. Fenn. Vanamo 3:185. 1948.

Type: Cameroons, Bipinde, corticole, G. Zenker (anno 1889).

Thallus epiphloeodal, smooth, continuous, pale ochraceous, K reddening. Stromata pulvinate, rounded to somewhat irregular, 1–2 mm. in diameter, about 0.8 mm. tall, containing (1–)2–4(–5) apothecia, discs very concave, 0.2–0.7 mm. in diameter, nude or slightly white-pruinose; parathecium black, entire, 125 μ thick on the sides, thinning to 75 μ thick below the hypothecium; hypothecium thick, I—; paraphyses discrete, branched, slender; asci cylindric, 1–3-spored, I—; ascospores hyaline, muriform, oblong, 120–160 $\times$ 24–30 μ, protoplasts spherical.

Our material is very old, having lost its thecia except for a single ascus adhering to the parathecium, showing three ascospores falling within the size range given by Räsänen.

Nigeria: Moor plantation near Ibadan, on *Theobroma,* C. A. Thorold 100, 101.

THELOTREMA

THELOTREMA Ach., Meth. Lich. 130. 1803.

Antrocarpum Meyer, Nebenstudien 326. 1825.

Volvaria Mass., Richerche Autonom. Lich. Crost. 141. 1852, probably not DC. 1805.

Coniochila Mass., Atti I. R. Ist. Veneto III, 5:258. 1860.

Schistostoma Stirton, Proc. Phil. Soc. Glasgow 11:312. 1879.

Type: not designated, but *Lichen lepadinus* would conserve the genus in the sense that it has been used for the last 150 years. *Antrocarpum* Meyer and *Volvaria* Mass. were also based on this species. *Coniochila* Mass. was based on *Thelotrema varioloides* Hampe *nom. nud.*, from Ceylon, not *T. varioloides* (Pers.) Ach. from Europe. From Massalongo's generic description, *T. varioloides* Hampe seems close to (if not identical with) *Schistostoma dehiscens* Stirton from South India, and closely related to *T. schistostomoides* Zahlbr. (*T. schistostoma* Müll. Arg. *non* Tuck.). *Schistostoma* Stirton was based on S. *dehiscens* Stirton.

Thallus epi- or endophloeodal, crustose, ecorticate or with an amorphous cortex; algae *Trentepohlia;* medulla usually loosely woven. Apothecia immersed in the substrate or in thalline warts; parathecium well developed, covering the thecium when young, then rupturing and forming an ostiole; paraphyses simple, unbranched; asci with 8 or fewer ascospores; ascospores hyaline, muriform with rounded protoplasts. Spermatia exobasidial, short-cylindric.

1. Ascospores solitary, 110–114 $\times$ 22–35 μ, 34-locular; columella subconic; thallus white, K red; Mozambique ..... *T. turgidulum* Vainio
1. Ascospores 2–4 per ascus, 185 $\times$ 22 μ, 42-locular; columella absent; thallus dark olive buff; Cameroons.... ..... *T. cameroonensis* Dodge
1. Ascospores 8 per ascus, under 25 μ long; columella not mentioned..... 2
   2. Thallus olivaceous; ascospores 18–25 $\times$ 5–10 μ, 8–10-locular, 2–3-locellate; Angola ..... *T. Pechuelii* Müll. Arg.
   2. Thallus pale yellowish; ascospores 14–25 $\times$ 7–9 μ; 4–6-locular; São Thomé..... ..... *T. foratum* Nyl.

Thelotrema (Pseudo-ascidium) **cameroonensis** Dodge, sp. nov.

Type: Cameroons, Banga, on *Theobroma,* C. A. Thorold 141.

Thallus epiphloeodes, 110–120 μ crassitudine, obscure olivaceo-alutaceus; cortex 55 μ crassitudine, hyphis pachydermeis periclinalibus, 5–6 μ diametro, exteris brunneis; stratum algarum 55–65 μ crassitudine, filamentis *Trentepohliae* minutis cum crystallis (rarius magnis) inter hyphas; medulla non evoluta. Apothecia in verrucis thallinis, 1–1.2 mm. diametro, 1 mm. altitudine, ostiolo non papillato; parathecium integrum, 210 μ crassitudine superne, ad 40 μ sub hypothecio tenuescens, non alatum, ostiolo 250 μ diametro, areola nigra, 200 μ latitudine circumdatum; hypothecium vix evolutum; thecium 430 μ altitudine; paraphyses tenues, flexuosae, ramosae, apicibus liberis; asci non bene visi; ascosporae binae vel quaternae, hyalinae, muriformes, ca. 42-loculares et 6-locellatae, 185 × 22 μ.

Thallus epiphloeodal, 110–125 μ thick, dark olive buff; cortex 55 μ thick, of thick-walled, periclinal hyphae 5–6 μ in diameter, the outer ones brownish; algal layer 55–65 μ thick, of filaments of *Trentepohlia* 6–7 μ in diameter, with many minute crystals and occasional larger ones; medulla not differentiated. Apothecia in thalline warts, 1–1.2 mm. in diameter, 1 mm. tall, ostiole not papillate, about 250 μ in diameter; parathecium exposed as a black area 200 μ wide around the ostiole, in turn surrounded by a paler area of about the same extent; parathecium carbonaceous, entire, 210 μ thick above, thinning to 40 μ below the hypothecium, not winged at the base, resting on the cork cells of the bark; hypothecium scarcely differentiated; thecium 430 μ tall; paraphyses slender, flexuous, branched, tips free in the thecial gel; asci not clearly seen, ascospores in pairs or fours in the thecial gel; ascospores hyaline, muriform, about 42-locular, 6-locellate, 185 × 22 μ.

Occasionally there are two confluent thalline warts with two ostioles but the apothecia are not crowded as in sect. *Tremotylopsis* Zahlbr.

OCELLULARIA

Ocellularia Meyer, Nebenstudien 327. 1825.

Thelotrema subg. *Ocellularia* Vainio, Etude Lich. Brésil 2:262. 1890.
Ascidium Fée, Essai Crypt. Ecorces Officin. xlii, 96. 1824.
Ocellularia sect. *Ascidium* Müll. Arg., Flora 64:525. 1881.
Myriotrema Fée, Essai Crypt. Ecorces Officin. xlix, 103. 1824.
Ocellularia sect. *Myriotrema* Zahlbr. in Engler & Prantl, Die Nat. Pflanzenfam. I. 1*:118. 1905.
Stegobolus Mont. in Hooker's London Jour. Bot. 4:4. 1845.
Ectolechia Mass., Alcuni Gen. Lich. 10. 1853, *non* Trev. 1853.
Brassia Mass., Atti I. R. Ist. Veneto III, 5:259. 1860.
Coscinedia Mass., Atti I. R. Ist. Veneto III, 5:256. 1860.
Chapsa Mass., Atti I. R. Ist. Veneto III, 5:257. 1860.
Ocellis Clements, Gen. Fung. 80. 1909.

Type: not designated. Two species were transferred from *Thelotrema* (*T. obturatum* and *T. urceolare,* both now in *Ocellularia*) and six from *Pyrenula,* all of which belong in *Pyrenula* as now used). *Ascidium* Fée was based on *A.*

Cinchonarum Fée. *Myriotrema* Fée was based on M. *olivaceum* and M. *album* Fée. *Stegobolus* Mont. was based on S. *Berkeleyanus* Mont. *Ectolechia* Mass. was based on *Ascidium rhodostoma* Mont. *Brassia* Mass. was based on *Thelotrema porinoides* Mont. & v. d. Bosch, now in *Ocellularia*. *Coscinedia* Mass. was based on *Thelotrema microporum* Mont., now in *Ocellularia*. *Chapsa* Mass. was based on *C. indicum* Mass. *Ocellis* Clements was a segregate for species with bilocular ascospores, and was probably based on *Ocellularia myriopora* (Tuck.) Müll. Arg., but the combination was not formally made.

Since *Ascidium* Fée and *Myriotrema* Fée are both older than *Ocellularia*, the last should be conserved, based on *Thelotrema obturata* or *T. urceolare*, in order to avoid a very large number of new combinations. However, it should be without prejudice of *Ascidium* and *Myriotrema*, if a future monographer decides to split the genus. Both names are already in use for very distinct sections of *Ocellularia*.

Thallus crustose, uniform, heteromerous; ecorticate or with an amorphous cortex; algae *Trentepohlia*. Apothecia more or less immersed in substrate or in thalline warts; parathecium and amphithecium covering the thecium when young, then rupturing stellately or forming a circular ostiole, or wholly breaking away above the usually white pruinose thecium; central columella present or absent; paraphyses unbranched; asci 1–8-spored; ascospores septate with lenticular protoplasts, hyaline.

1. Ascospores 4–6-locular 2
1. Ascospores 6–10-locular; thallus ashy, yellowish or fuscous 4
1. Ascospores 16 or more locular 5
   2. Thallus white; columella present in the thecium 3
   2. Thallus glaucous; columella absent; ascospores 6-locular, 45–53 × 11–14 μ; ostiole only 40 μ in diameter; Guinea ..... *O. trypanea* (Ach.) Dodge
   2. Thallus light olive-gray; ascospores 4(–6)-locular, 18–25 × 8–10 μ; ostiole 150 μ in diameter; São Thomé ..... *O. subterebrata* (Nyl.) Zahlbr.
3. Ascospores 4–5-locular, 15–17 × 6 μ; apothecia 0.5–1 mm. in diameter; Sierra Leone ..... *O. discoidea* (Ach.) Müll. Arg.
3. Ascospores 6–10-locular, 17–20 × 6–7 μ; ostiole 0.1–0.2 mm. in diameter; Mozambique ..... *O. mozambica* (Vainio) Zahlbr.
   4. Thallus yellowish, K red, margin indeterminate; ascospores 27–34 × 8–10 μ, 7–9-locular; Kenya ..... *O. Poncinsiana* Hue
   4. Thallus smoky-ashy; columella present; ascospores 20–30 × 7–8 μ, 6–8-locular; Sierra Leone ..... *O. fumosa* (Ach.) Müll. Arg.
   4. Thallus ashy fuscous to greenish; columella not mentioned; ascospores 25–43 × 6–8 μ, 8–10-locular; Sierra Leone ..... *O. cavata* (Ach.) Müll. Arg.
   4. Thallus darker olive; ascospores as in *O. cavata;* apothecia half the size, more depressed with a smaller ostiole, columella not mentioned; Sierra Leone ..... *O. obturata* (Ach.) Sprgl.
5. Ascospores 16-locular, 36–60 × 6–9 μ; thecium 90 μ tall; apothecia 0.5–1 mm.; thallus white; Mozambique ..... *O. albescens* (Vainio) Zahlbr.
5. Ascospores 22–30-locular, 50–60 × 3(–5.5) μ; thecium 135 μ tall; apothecia 0.4 mm.; thallus dark olive buff; Nigeria ..... *O. scolecospora* Dodge

Ocellularia subterebrata Zahlbr., Cat. Lich. Univ. 2:601. 1924.

Thelotrema subterebrata Nyl., Flora 69:174. 1886.

Type: São Thomé, Pico, 1500–2100 m., A. Möller, comm. J. Henriques.

Thallus epiphloeodal, light olive gray, 100 μ thick; cortex 6–8 μ thick, de-

composed; algae periclinal filaments of *Trentepohlia*, 5–6 μ, filling the rest of the thallus, closely packed and partly disorganized, and penetrating the bark at least 65 μ; medulla absent. Apothecia rather crowded but distinct, 0.3–0.4 mm. in diameter, lip elevated about 0.1 mm. above the surface of the thallus, innate, ostiole 150 μ in diameter; parathecium dimidiate, 55–60 μ thick, pale brownish, darker at the lips, of slender, interwoven, periclinal hyphae, nubilated with minute granules; hypothecium 12 μ thick, of conglutinate, interwoven periclinal hyphae; thecium 115 μ tall, 140 μ in diameter; paraphyses slender, not dense, once or twice dichotomous above the asci, tips clavate; asci 8-spored, cylindric, 95 $\times$ 15 μ; ascospores imbricately monostichous, hyaline, 6-locular, protoplasts slightly rounded, 16 $\times$ 5–6 μ.

Our material, described above, has slightly smaller ascospores but as Nylander stated, has the appearance of O. *microspora*. Nylander also stated "subsimilis *T. terebratae*," but it is not clear if this implies the presence of a columella which is lacking in our material.

Sierra Leone: Kenema (Nongowa), on *Copaifera copallifera*, F. C. Deighton M5012.

OCELLULARIA **trypanea** Dodge, comb. nov.

Pyrenula trypanea Ach., Syn. Lich. 119. 1814.
Verrucaria trypanea Sprgl., Syst. Veg. 4:1:244. 1824.

Type: Guinea, corticole, Afzelius.

Thallus epiphloeodal, 135 μ thick, deep sea-foam green; cortex scarcely differentiated, 5–6 μ thick, of two layers of conglutinate, periclinal hyphae; algal layer about 130 μ thick, usually a narrow layer 20 μ thick, nearly separated by a layer of coarse crystals from the main layer 65 μ thick next the bark cells, of more or less vertical filaments of *Trentepohlia* 5–6 μ in diameter. Apothecia crowded, perithecioid, opening by an ostiole about 40 μ in diameter, surrounded by a narrow blackened area, immersed in thalline warts, about 1 mm. in diameter and 0.3 mm. tall; parathecium hyaline (pale yellowish in thick sections), 13–14 μ thick, of conglutinate, periclinal hyphae, surrounded by the algal layer of the thallus; hypothecium 15 μ thick, of slender, densely woven hyphae; thecial gel filling the cavity, paraphyses somewhat dichotomously branched, tips free, not compact; asci clavate, thin-walled when young, 8-spored; ascospores hyaline, fusiform, 6-locular, protoplasts rounded, 45–53 $\times$ 11–14 μ.

The thallus and very thin, hyaline parathecium clearly relate this species to the Thelotremaceae rather than to the Pyrenulaceae, although the habit and cross-section suggest the Pyrenulaceae, especially with the low magnifications available to Acharius. In old apothecia, the thecial gel turns brown, agreeing with Acharius' observation. On the other hand, I have not found the ostiole clearly papillate at any stage as reported by Acharius.

Nigeria: Ondo Province, Erinmo, on *Theobroma*, C. A. Thorold 134.

OCELLULARIA CAVATA Müll. Arg., Flora 65:499. 1882.

Thelotrema cavata Ach., K. Vetensk. Akad. Nya Handl. 33:92. 1812.

Type: Sierra Leone, corticole, Afzelius.

Thallus cartilaginous, verrucose, wrinkled, ashy greenish-fuscous. Apothecia gibberulous, margin of broad ostiole entire, tumid, somewhat verrucose, disc black, covered with a glaucous pruina; parathecium black; ascospores 25–43 × 6–8 μ, (6–)8–10-locular, *fide* Müller Argau.

In our collections, a single thallus may belong here. The thallus agrees in color with Acharius' description (deep olive buff) and is 125–185 μ thick, cortex about 25 μ thick, of thin-walled, conglutinate, mostly periclinal hyphae; algal layer 15 μ thick, continuous, of short filaments of *Trentepohlia*, 5–6 μ in diameter, partly disorganized; medulla 85–145 μ thick, of thick-walled, closely interwoven hyphae, penetrating deeper between blackened cork cells. Apothecia 0.5–0.7 mm. in diameter, 0.3 mm. tall, flattened above and coarsely white-granular, easily mistaken for a member of the *Pertusaria velata* group when the thecium is replaced by soredia. Parathecium about 25 μ thick, hyaline, of large-celled pseudoparenchyma surrounded by a yellow layer 20 μ thick, of disintegrated bark cells and very minute crystals, which is in turn surrounded by a thin layer of thallus. The thecium has disintegrated and been replaced by huge crystals 65 × 25 μ or more. Near the parathecium in a bit of disintegrated thecium, a single ascospore 37 × 8 μ was found with 8 rounded protoplasts, well within the range of size reported by Müller Argau.

Nigeria: Abdo Ekiti near Ondo, on *Theobroma*, C. A. Thorold 139.

OCELLULARIA **scolecospora** Dodge, sp. nov.

Type: Nigeria, Moor plantation near Ibadan, on *Theobroma*, C. A. Thorold 160.

Thallus hypophloeodes, obscure olivaceo-alutaceus, ex isidiis granularibus 15–25 μ diametro; stratum algarum 25 μ crassitudine, 25 μ sub superficie corticis *Theobromatis*, filamentis *Trentepohliae* 5–6 μ diametro, periclinalibus inter cellulas suberosas. Apothecia orbicularia, 150 μ altitudine, 400 μ latitudine, sine columella, non aut parce basi constricta, erumpentia, disco albo-pruinoso; pseudo-amphithecium 25 μ crassitudine, cellulis suberosis, hyphis paucis cellulisque *Trentepohliae;* parathecium 15–25 μ crassitudine, integrum, hyphis pachydermeis, periclinalibus, fuligineis, lateribus verticalibus intus cum cellulis hyalinis magnis laxis; hypothecium vix evolutum; thecium 135 μ altitudine; paraphyses tenues, subdichotome ramosae, rarissime anastomosantes, apicibus non incrassatis, pruina crystallorum tectae; asci fusiformes, 130 × 15 μ; ascosporae octonae, hyalinae, 22(–30)-loculares, protoplastis rotundatis, curvatae vel flexuosae, 50–66 × 3(–5.5) μ.

Thallus hypophloeodal, dark olive buff, from minute granular isidia, 15–25 μ in diameter; algal layer about 25 μ thick, situated about 25 μ below the surface of the bark, filaments of *Trentepohlia*, 5–6 μ in diameter, periclinal between the cork cells, somewhat disorganized, with occasional filaments above and below the main

layer, the lower cork cells blackened, forming a layer 15 μ thick. Apothecia round, 150 μ tall, about 400 μ broad, without a columella, not or slightly constricted at the base, disc densely white-pruinose, carrying a layer of cork cells 25 μ thick, with hyphae and a few algal cells up to the top of the parathecium, thus forming a pseudo-amphithecium; parathecium 15–25 μ thick, entire, of dark fuliginous, periclinal, thick-walled hyphae, appearing carbonaceous in thick sections, inside which is a nearly hyaline layer of very large, loosely packed cells; hypothecium scarcely differentiated; thecium 135 μ tall; paraphyses slender, somewhat dichotomously branched and anastomosing in the thecial gel, tips not thickened, covered with a thick pruina of crystals (which mostly wash away in sectioning and mounting); asci fusiform, about 8-spored, 130 $\times$ 15 μ; ascospores hyaline, fusiform, 22–30-locular, protoplasts rounded, 50–66 $\times$ 3(–5.5) μ, when free from the ascus, breaking apart into short sections of 6–8 cells, flexuous or curved, twisted about each other in the ascus.

Perhaps this species should be taken as the type of a new genus, homologous with *Gyrostomum* Fr. in the series with brown, muriform ascospores. The spore measurements are rather unsatisfactory, as I have been unable to free whole spores from the ascus without breaking them. In the ascus they are so twisted about each other that I have been unable to see both ends at once. In *Thorold 161* and *117*, the ascospores are less twisted in the ascus and measure approximately 50–66 $\times$ 3 μ and are at least 30-septate.

This species differs from *O. albescens* (Vainio) Zahlbr. in lacking a columella, a darker thallus, a taller thecium, and narrower, more septate ascospores.

Nigeria: Moor plantation near Ibadan, C. A. Thorold 160, type; Ina near Ibadan, C. A. Thorold 162; Ondo Province, Owena near Akure, C. A. Thorold 117, 161, 163; Abdo Ekiti, C. A. Thorold 118; Akure, C. A. Thorold 162; all on *Theobroma*.

Gyalectaceae

Thallus crustose, homoeomerous or heteromerous, usually ecorticate, with *Trentepohlia* or *Phyllactidium* algae. Apothecia immersed to sessile, solitary; amphithecium often present; parathecium hyaline (dark in *Sagiolechia*); asci 8–many-spored; ascospores hyaline, from unicellular to muriform, with thin septa and cylindric protoplasts when septate and cubical protoplasts when muriform.

1. Corticole or saxicole, with *Trentepohlia* algae 2
1. Foliicole with *Phyllactidium* algae 6
2. Asci 6–8-spored 3
2. Asci 12–many-spored 5
3. Parathecium dark, entire ..... *Sagiolechia* Mass.
3. Parathecium hyaline or light-colored, waxy 4
4. Ascospores unicellular ..... *Ionaspis* Th. Fr.
4. Ascospores bilocular ..... *Dimerella* Trev. (*Microphiale* Zahlbr.)
4. Ascospores 4 or more locular ..... *Secoliga* Norm.
4. Ascospores muriform ..... *Gyalecta* Ach.
5. Ascospores bilocular, fusiform ..... *Ramonia* Stzbgr.
5. Ascospores 6–pluri-locular, fusiform to acicular ..... *Pachyphiale* Lönnr.
6. Ascospores bilocular ..... *Lecaniopsis* Zahlbr.
6. Ascospores 4-locular, acicular ..... *Semigyalecta* Vainio

IONASPIS

IONASPIS Th. Fr., Lichenogr. Scand. 1:273. 1871.

Type: not designated, seven species listed, all still included in recent monographs.

Thallus crustose, uniform or effigurate, epi- or endolithic (epiphloeodal in *I. ascidioides*), homoeomerous, algae *Trentepohlia.* Apothecia immersed to adnate; parathecium pale or dark; paraphyses simple or sparingly branched above; asci clavate, 8-spored; ascospores unicellular, hyaline, ellipsoidal with a thin wall. Spermatia short, cylindric, straight.

IONASPIS **ascidioides** Dodge, sp. nov.

Type: Nyasaland, Kasungu Hill, 1100 m., L. J. Brass 17458a′.

Thallus epiphloeodes, minute verrucosus, rimulosus, 150–175 μ crassitudine, albidus, anguste nigro-marginatus; ecorticatus; filamentis *Trentepohliae* 8 μ diametro, dense aggregatis, verticalibus, lacunis sphaericis exceptis, 40–80 μ diametro, crystallis magnis hyalinis impletis; medulla non evoluta. Apothecia 0.5–0.6 mm. diametro, sessilia, basi constricta, margine crasso involuto dein tenuiori et thecio aequante, integro aut verticaliter striolato; discus nigro-brunneus, dense albo-pruinosus; amphithecium 90 μ crassitudine, stratum algarum 40 μ crassitudine, filamentis periclinalibus, stratum interius lacunis, magnis cum crystallis; parathecium integrum, hyalinum, pseudoparenchymaticum, 18–24 μ crassitudine; hypothecium 10 μ crassitudine, hyphis tenuibus; thecium 65 μ altitudine; paraphyses conglutinatae, tenues, dichotome ramosae, apicibus non incrassatis, brunneis; asci clavati dein cylindrici, pachydermei, 55 × 14 μ; ascosporae octonae (an 12nae?), hyalinae, uniloculares (juventute false biloculares), leptodermeae, 8–9 × 6–7 μ.

Thallus epiphloeodal, minutely verrucose, rimulose, 150–175 μ thick, whitish with a very narrow black margin; ecorticate; algae *Trentepohlia,* filaments vertical, closely packed except for more or less spherical lacunae, 40–80 μ in diameter, filled with large hyaline crystals. Apothecia 0.5–0.6 mm. in diameter, constricted at the base, margin thick and inrolled when young, becoming thinner and level with the very dark brown, densely white, pruinose disc, entire, becoming slightly vertically striolate; amphithecium 90 μ thick, of an algal layer 40 μ thick of periclinal filaments, the rest of the lacunae filled with large crystals; parathecium entire, hyaline, of small-celled pseudoparenchyma, 18–24 μ thick; hypothecium 10 μ thick, of slender, deeply staining hyphae; thecium 65 μ tall; paraphyses conglutinate, slender, dichotomous, tips not thickened in the brown epithecial gel; asci clavate-cylindric, thick-walled, tip of protoplast acute to mamillate, 8(–12?)-spored, 55 × 14 μ; ascospores hyaline, unicellular, falsely bilocular when young, wall thin, 8–9 × 6–7 μ.

The thallus and amphithecium with large lacunae filled with very large crystals and the shape of the apothecium suggest a relationship to *Ocellularia* subg. *Ascidium* of the Thelotremaceae, which has quite different ascospores. The algae are clearly filamentous *(Trentepohlia)*, hence exclude this species from *Lecanora.*

I have hesitated to refer this species to *Ionaspis,* which is otherwise saxicolous with immersed apothecia so that the older species were first described in *Lecanora* subg. *Aspicilia,* but the homoeomerous thallus with *Trentepohlia* algae, as well as the spores, seems definitely to belong here, unless one enlarges the concept of the Thelotremaceae to include a new genus with unicellular ascospores. The mature spore is certainly unilocular, although young ascospores have a narrow zone of deeply staining granules across the middle, making them appear falsely bilocular, as one often sees in the Antarctic species of *Lecidea.*

SECOLIGA

Secoliga Norm., Nyt Mag. Naturvidensk. 7:230. 1853.

Cryptolechia Mass., Alcuni Gen. Lich. 13. 1853.
Phialopsis Koerber, Syst. Lich. Germ. 169. 1854.
Bryophagus Nitschke in Arn., Flora 45:38. 1862.
Gyalecta sect. *Secoliga* Tuck., Syn. N. Amer. Lich. 1:218. 1882.

Type: not designated. Of the six species included, *Lichen ruber* Hoffm. may be chosen, as it best fits the generic description. *Phialopsis* Koerb. was also based on this species. *Cryptolechia* Mass. was based on *Lecanora carneolutea* Ach. *Bryophagus* Nitschke was based on *B. Gloeocapsa* Nitschke.

Thallus crustose, uniform, epilithic, growing over mosses, or corticole; ecorticate; algae *Trentepohlia;* medulla loosely woven. Apothecia long immersed in the thallus then becoming sessile; parathecium waxy or horny, light-colored, nude or more usually covered by an amphithecium, disc concave; paraphyses unbranched; asci 8-spored; ascospores fusiform to ellipsoidal, septate with cylindric protoplasts. Spermatia exobasidial, cylindric, straight.

1. Ascospores 6-locular, 16–18 × 3 μ; thallus deep olive buff; apothecia 0.3–0.7 mm. in diameter, disc yellow ochre to clay color; Sierra Leone.....*S. Deightoni* Dodge
1. Ascospores 4–8-locular, 18–30 × 4–5 μ; thallus ashy.....2
   2. Apothecia 0.3–0.5 mm., disc reddish flesh-color; Usambara.....*S. versicolor* Müll. Arg.
   2. Apothecia 0.6–0.8 mm., disc whitish; Angola.....*S. plurilocularis* (Vainio) Dodge

Secoliga plurilocularis Dodge, comb. nov.

Gyalecta plurilocularis Vainio, Cat. Welwitsch Afric. Pl. 2:427. 1901.

Secoliga Deightoni Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on pebbles, F. C. Deighton M4840.

Thallus epilithicus, laevis, partim subrimulosus, 80 μ crassitudine, olivaceo-alutaceus, homoeomerus; filamentis *Trentepohliae* periclinalibus, 7–8 μ diametro. Apothecia sessilia, basi constricta, 0.3–0.7 mm. diametro, disco ochraceo-argillaceo, margine pallidiori; parathecium 65 μ crassitudine, superne ad 40 μ tenuescens, pseudoparenchymate cellulis radiantibus, pachydermeis, 4–6 μ diametro; hypothecium 55 μ crassitudine, brunneum, hyphis tenuibus, 3 μ diametro, periclinalibus, leptodermeis; thecium 65–80 μ altitudine; paraphyses conglutinatae, apicibus non incrassatis, brunneis, subdichotome ramosae super ascos; asci pachydermei, clavati, vel cylindrici, 60 × 16 μ; ascosporae octonae, hyalinae, leptodermeae, fusiformes, 6-loculares, 16–18 × 3 μ.

Thallus epilithic, smooth, partly subrimulose, 80 μ thick, deep olive buff, homoeomerous; algae *Trentepohlia,* filaments mostly periclinal, 7–8 μ in diameter. Apothecia sessile, constricted at the base, 0.3–0.7 mm. in diameter, disc yellow ochre to clay color, margin paler; parathecium 65 μ thick below, thinning to 40 μ above, hyaline, of radiating pseudoparenchyma, thick-walled cells 4–6 μ in diameter; hypothecium 55 μ thick, brownish, of thin-walled, mostly periclinal hyphae 3 μ in diameter; thecium 65–80 μ tall; paraphyses conglutinate, tips not thickened in the brownish epithecial gel, somewhat dichotomous above the asci; asci 8-spored, clavate-cylindric, thick-walled, 60 × 16 μ; ascospores hyaline, thin-walled, fusiform, 6-locular, 16–18 × 3 μ.

Coenogoniaceae

Thallus spongy-byssoid, adnate or forming dimidiate, shelving masses; homoeomerous with *Trentepohlia* or *Cladophora,* whose filaments are only partially surrounded by hyphae. Apothecia with pseudoparenchymatous parathecium; asci 8-spored; ascospores hyaline, uni- or bilocular; spermatia exobasidial.

Thallus with *Trentepohlia* ..... *Coenogonium* Ehrenb.
Thallus with *Cladophora,* apothecia unknown ..... *Racodium* Pers.

COENOGONIUM

Coenogonium Ehrenb. in Nees, Horae Phys. Berol. 120. 1820.

Type: *C. Linkii* Ehrenb.

Thallus loosely spongy-byssoid, either adnate or forming dimidiate shelving masses (suggesting a thin species of *Polystictus* in shape but not in texture), homoeomerous with *Trentepohlia* filaments partially covered by a network of hyphae. Apothecia scattered on the upper surface, scutiform, usually with a very short stipe; parathecium of thin-walled pseudoparenchyma; paraphyses unbranched, often with swollen tips; asci clavate, 8-spored; ascospores hyaline, fusiform or long-ellipsoid, 1–2-celled.

Coenogonium **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on trunk of *Phyllanthus discoideus,* F. C. Deighton M4396a.

Thallus tenuissimus, filamentis repentibus *Trentepohliae* 26 μ diametro, cellulis 75 μ longis, cylindricis, hyphis tenuibus, 3 μ diametro, partim corticatis. Apothecia 0.5–0.6 mm. diametro, in filamentis sessilia, juventute urceolata, dein plana, disco cinnamomeo-brunneo, margine subpallidiori, maturitate non elevato; parathecium inferne 55 μ crassitudine, non superne tenuescens, dimidia parte extera pseudoparenchymate radiante, pachydermeo, cellulis ca. 5 μ diametro, extus granulis flavis insperso, dimidia parte interna hyphis tenuibus periclinalibus dense contextum; hypothecium vix evolutum; thecium 40 μ altitudine; paraphyses tenues, conglutinatae, apicibus moniliformibus sed non incrassatis; asci clavati, 25 × 5 μ; ascosporae octonae, fusiformes, hyalinae, uniloculares, 6–8 × 2.5–3 μ.

Thallus very thin, of repent filaments of *Trentepohlia* 26 μ in diameter, corticate, with hyphae 3 μ in diameter. Apothecia 0.5–0.6 mm. in diameter, sessile on the algal filaments, urceolate at first, becoming plane, disc cinnamon brown, margin slightly lighter, not elevated at maturity; parathecium 55 μ thick below the hypothecium, not thinning above; the outer half composed of radiating thick-walled pseudoparenchyma, cells up to 5 μ in diameter, the outer 15 μ inspersed with yellow granules, the inner half of slender, periclinal, densely interwoven hyphae; hypothecium scarcely differentiated from the inner layer of the parathecium; thecium 40 μ tall; paraphyses slender, unbranched, conglutinate, tips moniliform but not thickened; asci clavate, 8-spored, about 25 $\times$ 5 μ; ascospores hyaline, fusiform, unilocular, 6–8 $\times$ 2.5–3 μ.

Coenogonium **congensis** Dodge, sp. nov.

Type: Belgian Congo, Yangola, 20 km. west of Yangambi, on twigs of *Ouratea brunneo-purpurea* Gilg, J. Louis 12070.

Thallus dimidiatus, radius 1 cm., filamentis *Trentepohliae* 5–6 μ diametro, cellulis ad 8 μ longitudine. Apothecia convexa, sessilia in filamentis, ad 1 mm. diametro, disco ochraceo-aurantiaco, margine concolore, subdentato; parathecium 135 μ crassitudine sub hypothecio, superne ad 105 μ tenuescens, dimidia parte extera hyphis rectis septatis, pachydermeis, hyalinis extus subbrunneis, pseudoparenchyma formante, dimidia parte interna hyphis pachydermeis periclinalibus; hypothecium vix evolutum, 10 μ crassitudine, subbrunneum; thecium 55 μ altitudine; paraphyses tenues, conglutinatae, apicibus pallide brunneis non incrassatis; asci cylindrici, 50 $\times$ 3 μ; ascosporae octonae, monostichae, fusiformes, biloculares, hyalinae, leptodermeae, 6 $\times$ 2.5 μ.

Thallus dimidiate, radius 1 cm., of filaments of *Trentepohlia* 5–6 μ in diameter, cells about 8 μ long. Apothecia convex, sessile on the algal filaments, up to 1 mm. in diameter, disc ochraceous orange, margin concolorous, slightly dentate; parathecium 135 μ thick below, thinning to 105 μ thick at the margin, outer half of vertical, thick-walled, septate hyphae 4 μ in diameter, forming a pseudoparenchyma, hyaline, the outer 8 μ slightly brownish, the inner half of thick-walled, densely woven periclinal hyphae; hypothecium scarcely differentiated, represented by a slightly brownish layer about 10 μ thick; thecium 55 μ tall; paraphyses slender, unbranched, conglutinate, tips not thickened in the pale brown epithecial gel; asci 8-spored, cylindric, about 50 $\times$ 3 μ; ascospores monostichous, fusiform, bilocular, hyaline, very thin-walled, 6 $\times$ 2.5 μ.

Collemaceae

Thallus gelified, crustose to foliose or dwarf-fruticose, with or without rhizinae; ecorticate or corticate with one or two layers of isodiametric cells. Apothecia immersed to sessile, amphithecium often present; parathecium often rudimentary when the amphithecium is well developed; paraphyses unbranched; asci 8-spored; ascospores hyaline or pale brownish, ellipsoidal to fusiform or acicular, unicellular to muriform.

Besides the species of *Collema* included below, there are a few scraps of at least two species of *Leptogium*, one completely unidentifiable and the other in the *L. vesiculosum* group, probably not that species and too meagre for description. The other tropical genera are small and seldom collected.

COLLEMA

COLLEMA Wiggers, Primit. Fl. Holsat. 89. 1780.

Lathagrium S. F. Gray, Nat. Arr. Brit. Pl. 1:399. 1821.
Lethagrium Mass., Mem. Lichenogr. 90. 1853.
Synechoblastus Trev., Caratt. Tre Nuov. Gen. Collemac. 3. 1853.
Blenothallia Trev., Caratt. Tre Nuov. Gen. Collemac. 3. 1853.

Type: *C. Lactuca* (Web.) Wiggers, a synonym of *Lichen crispus* L. now in sect. *Blenothallia*. *Lathagrium* S. F. Gray was based on *C. flaccidum* Ach., *C. nigrescens* (Huds.) DC., both in sect. *Collemodiopsis* Vainio, and *C. scotinum* Ach., later transferred to *Leptogium*. *C. nigrescens* may be chosen as type if the section *Collemodiopsis* is raised to generic rank. *Lethagrium* Mass. is probably only a variant spelling of *Lathagrium*. It included *C. fasciculare* Wigg., *C. rupestre* (Sw.) Rabh., *C. ascaridiosporum* Mass., *C. conglomeratum* Mass. and *C. turgidum* Ach., the last now placed in *Leptogium*. *Synechoblastus* Trev. was based on *C. aggregatum* (Ach.) Röhl., *C. nigrescens* (Huds.) DC., and *C. rupestre* (Sw.) Rabh. Since the latter two species belong in the section *Collemodiopsis*, *C. aggregatum* may be chosen as the type when *Synechoblastus* is used as a separate genus. *Blenothallia* Trev. was based on *C. cheilea* Ach. and *C. haemaleia* Smrft., the latter now placed in *Pyrenopsis*.

Thallus squamulose to foliose, gelified, without rhizinae, homoeomerous; ecorticate (except the amphithecium in sect. *Collemodiopsis*); algae *Nostoc*, hyphae loosely arranged in the algal gel. Apothecia immersed at first then erumpent, sessile to scutellate, constricted at the base; amphithecium well developed, parathecium present but more or less rudimentary; paraphyses simple, septate; asci 8-spored; ascospores acicular, fusiform or ellipsoidal (2-locular in sect. *Dicollema*, 3–pluri-locular in sect. *Collemodiopsis* and *Synechoblastus*), broadly ellipsoid and dwarf-muriform in sect. *Blenothallia*.

COLLEMA NIGRESCENS (Huds.) DC. var. MINUTUM Hue, Mém. Soc. Bot. France 8:130. 1910.

Type: French Tropical Africa, Chari, Baguirmi, corticole, A. Chevalier.

Thallus dark olive, foliose, membranous, 32 μ thick, monophyllous, 2–4 cm. in diameter, lobes 0.4–12 mm. broad, radiating, contiguous or somewhat imbricate, tips rounded, surface smooth with radiating wrinkles, paler beneath, costate, partly clinging to the underlying bark by hyphae, but not developed into rhizinae. Hyphae 2–3.75 μ, mostly perpendicular to the surface of the thallus, thin-walled, sparsely septate, in the center of the thallus periclinal and forming a loose medulla about 20 μ thick, without algae. At the surface a few periclinal hyphae forming a

highly gelified and almost amorphous cortex 8–10 μ thick, in contrast to the clearly cellular cortex of *Leptogium;* algae *Nostoc*, cells 2.5–3.75 μ in diameter, in curved, moniliform chains. Apothecia 0.4–0.6 mm. in diameter, at first immersed in the thallus, then short-pedicellate, disc rufous, plane to convex; cortex in amphithecium and pedicel 15–20 μ thick, of cells 8–10 μ in diameter, with thalline hyphae radiating between the parathecium and the amphithecial cortex between the algal colonies; parathecium hyaline, 50–80 μ thick below the thecium, thinning to 20 μ on the sides and 10 μ at the top, cells 5–15 (–18) μ in diameter below the thecium, smaller and less conspicuous above; hypothecium 40 μ thick, of densely woven, periclinal hyphae; thecium 100 μ tall; paraphyses 4–5 μ in diameter, thick-walled, lumen 1.5–1.7 μ, up to 3 μ in the terminal cell; asci 8-spored, clavate, tips thickened, 75 $\times$ 12 μ; ascospores hyaline, fusiform, 4-locular, 27–32 $\times$ 4–5 μ.

In this small variety, the ascospores are smaller, as those of the species are about 34–42 $\times$ 5 μ.

Nigeria: Agbaola and Ajia near Ibadan, on *Theobroma,* C. A. Thorold 114, 115, respectively.

Cameroons: Tombel, on *Theobroma,* C. A. Thorold.

LECIDEACEAE

Thallus crustose, uniform or with effigurate margins, continuous, areolate or squamulose (foliose in *Psora* and dwarf-fruticose in *Sphaerophoropsis*), attached to the substrate by hyphae of the medulla or hypothallus, without rhizinae; ecorticate or with a cortex of fasciculate, thick-walled hyphae, never pseudoparenchymatous; algae *Protococcus* or *Trebouxia;* medulla loosely woven or with a basal layer suggesting the structure of the upper cortex. Apothecia round, sessile, occasionally immersed or with a very short stalk; amphithecium absent; parathecium entire or dimidiate, hyaline or carbonaceous; hypothecium hyaline; paraphyses simple or sparingly forked above the asci, free or conglutinate; asci usually 8-spored (fewer than 8 in *Mycoblastus* and *Megalospora,* or 16–32 in a few species of *Lecidea* and *Bacidia*); ascospores hyaline (brown in *Rhizocarpon*), unilocular, septate or muriform, with or without a halo. Spermogonia immersed, spermatiophores unicellular; spermatia elongate-ellipsoid to cylindrical, often very long.

1. Ascospores unicellular 2
1. Ascospores septate 3
1. Ascospores muriform 6
   2. Ascospores small and thin-walled, uninucleate ..... *Lecidea* Ach.
   2. Ascospores very thick-walled and large, multinucleate ..... *Mykoblastus* Norm.
3. Ascospores bilocular 4
3. Ascospores 4–pluri-locular 5
   4. Ascospores under 30 μ long, slender, thin-walled ..... *Catillaria* Th. Fr.
   4. Ascospores over 40 μ long, stout, thick-walled ..... *Megalospora* Mey. & Fw.
5. Thallus ecorticate, smooth or more often granular ..... *Bacidia* DNtrs.
5. Thallus corticate, verrucose to subsquamulose ..... *Toninia* Mass.
   6. Paraphyses unbranched; ascospores hyaline ..... *Lopadium* Koerb.
   6. Paraphyses branched; ascospores brown with halo ..... *Rhizocarpon* Ram.

LECIDEA

LECIDEA Ach., Meth. Lich. 32. 1803.

Type: not designated. It is probable that when we have a modern monographic treatment of this genus, it will be divided into several genera on the morphology of the apothecium. Until then, it seems best not to select a type species from the many included in the genus when it was segregated from *Lichen* L. Most of those included belong in *Lecidea* as now recognized.

Thallus crustose, continuous, areolate, verrucose, attached to the substrate by hyphae of the medulla or hypothallus, without rhizinae; ecorticate or with a thin cortex, sometimes sorediose, very rarely with true soralia; algae protococcoid. Apothecia round or angular from mutual pressure, very rarely slightly elongate, immersed, sessile or very short-stalked; parathecium hyaline, colored or black, entire or dimidiate; hypothecium hyaline or somewhat brownish; epithecium bright-colored or black; paraphyses unbranched or sparingly so above the asci; asci usually 8-spored, rarely 16-spored; ascospores hyaline, unicellular (sometimes falsely bilocular), spherical, ellipsoid or allantoid. Spermogonia immersed, with a dark mouth, spherical; spermatiophores unicellular; spermatia short-cylindric to filiform, straight or curved.

All of our material belongs in the subgenus *Biatora* with hyaline or brightly colored, more or less waxy parathecium and colored disc, sometimes darkening in age, usually corticolous or lignicolous. For completeness, I have included a key to the subgenus *Eulecidea* with a very dark, usually carbonaceous parathecium and black disc, usually saxicolous.

1. Parathecium light-colored, waxy, never carbonaceous, disc reddish, yellowish fuscous to very dark brown (almost black); corticolous (very rarely saxicolous); subg. BIATORA.....2
1. Parathecium very dark brown, usually carbonaceous, disc black or greenish black; saxicolous or terricolous; subg. EULECIDEA.....16
   2. Ascospores 16–32 per ascus, 5–8 × 2–3 μ; thallus granular-furfuraceous; apothecia 0.5–0.9 mm., dark fuscous, entire; São Thomé.....*L. furfurosula* Nyl.
   2. Ascospores 8 per ascus 3
3. Disc somewhat white-pruinose, hair-brown (benzo brown to fuscous when pruina is rubbed off); parathecium hyaline; hypothecium fuliginous above; thallus of hemispheric warts with a black margin; medulla yellowish; Guinea.....*L. granifera* (Ach.) Vainio
3. Disc not white-pruinose 4
   4. Disc testaceous, flesh-color, reddish, rarely yellowish when young.....5
   4. Disc fuscous 11
   4. Disc almost black 13
5. Ascospores 4.5–6 × 2–3 μ; thallus olive green; disc flesh-red; hypothecium yellowish-hyaline; Usambara .....*L. pannosa* Müll. Arg.
5. Ascospores 8–11 × 2–4 μ.....6
5. Ascospores larger and broader; thallus ashy 7
   6. Thallus ashy to chalky white; disc plane, pale yellow flesh-color; ascospores 7–9 × 2–3 μ; Usambara .....*L. microspermoides* Müll. Arg.
   6. Thallus ashy glaucous; disc dark red, convex; ascospores 8–9 × 4 μ; Angola.....*L. cinereorubra* Vainio
   6. Thallus dark ashy to clay color; disc subvitelline, becoming fuscous-fleshcolor, convex; ascospores 8–11 × 2–2.5 μ; Angola.....*L. tenuis* Müll. Arg.

7. Apothecia 0.3–0.7 mm., disc rufous-fleshcolor, plane; ascospores 13–14 × 6–7.5 μ; Kenya ..... *L. carneorufa* Müll. Arg.
7. Apothecia 0.5–0.6 mm., disc buckthorn brown; hypothecium pale brownish; ascospores 8–11 × 4–5.5 μ; Nigeria ..... *L. nigeriensis* Dodge
7. Apothecia 0.5–1.2 mm., disc testaceous or yellowish 8
8. Parathecium entire, black below, disc testaceous; ascospores 15 μ long; medulla yellow; Usambara ..... *L. hypomeloides* Müll. Arg.
8. Parathecium entire, outer half hyaline, inner half fuliginous, disc isabelline; ascospores 11–12 × 5–6 μ; medulla white; Guinea ..... *L. rubina* Ach.
8. Parathecium dimidiate, at least pale below, disc testaceous; Angola 9
9. Hypothallus black; ascospores 9–12 × 6–8 μ ..... *L. caliginosa* v. *rhacocarpa* Vainio
9. Hypothallus white or inconspicuous 10
10. Ascospores 9–14(–17) × 4–5 μ; parathecium pale ..... *L. gyalectoides* Vainio
10. Ascospores 8–12 × 5–7 μ; parathecium fuscescent ..... *L. capopensis* Vainio
11. Hypothecium fuscous black; apothecia 0.5–0.8 mm.; ascospores 12–16 × 6–7 μ; Erythaea ..... *L. albocincta* Vainio
11. Hypothecium hyaline 12
12. Thecium yellowish; apothecia 0.5–0.75 mm.; ascospores 9–11 × 4–5 μ; Kenya ..... *L. endochrysea* Müll. Arg.
12. Thecium hyaline; apothecia 0.3 mm.; ascospores 9–11 × 6–7 μ; Ilha Principe ..... *L. citima* Nyl.
12. Thecium hyaline; apothecia 1 mm.; ascospores 12 × 6 μ; Usambara ..... *L. phaeophthalma* Zahlbr.
13. Apothecia 0.4–0.5 mm.; thecium 45 μ tall; ascospores 7–15 × 3–5 μ; Angola ..... *L. Sangeana* Vainio
13. Apothecia 0.5 mm.; ascospores 11–13 × 8–9 μ; saxicole; Kenya [may belong in Eulecidea] ..... *L. trachytica* Müll. Arg.
13. Apothecia 0.7–1.6 mm. 14
14. Thallus white-punctate; thecium 75–84 μ tall; ascospores 12 × 6 μ; Usambara ..... *L. phaeophthalma* Zahlbr.
14. Thallus smooth; thecium 60–65 μ tall; ascospores 15 × 4.5 μ; Usambara ..... *L. amaniensis* Zahlbr.
14. Thallus verruculose to granulose; Angola 15
15. Ascospores 9–13 × 6–7 μ ..... *L. nigricans* Vainio
15. Ascospores 8–9 × 6.5–7 μ ..... *L. mossamedana* Vainio
16. Apothecia innate, parathecium little developed [may belong in *Aspicilia*] 17
16. Apothecia emersed to sessile 19
17. Thallus white, immarginate; apothecia 0.5–0.9 mm., disc chalky pruinose; parathecium dark, hypothecium hyaline; Angola ..... *L. lithagoga* (Nyl.) Vainio
17. Thallus pale glaucous; apothecia 1 mm.; disc black; parathecium and hypothecium umber fuscous; Kenya ..... *L. glauconigra* Steiner
17. Thallus yellow ashy; disc black; parathecium hyaline 18
18. Thallus black-margined; apothecia 0.15–0.25 mm.; ascospores 8–11 × 4–4.5 μ; Angola ..... *L. angolensis* Müll. Arg.
18. Thallus not black-margined; apothecia 0.3(–0.4) mm.; ascospores 9–13 × 5–6.5 μ; Kenya ..... *L. angolensis* v. *orientalis* Steiner
19. Thallus squamulose at the margin, gray or white; Central Africa 20
19. Thallus leprose-granulose, yellowish; apothecia 0.13–0.3 mm., disc black, parathecium entire, fuscous; ascospores 8–9 × 6–7 μ; Kenya ..... *L. xanthinula* Müll. Arg.
19. Thallus dispersed, glebous, pale glaucous; apothecia 0.5 mm., disc black; parathecium entire, hyaline but top of thecium blue-green; ascospores 11–13 × 8–9 μ; Kenya ..... *L. trachytica* Müll. Arg.
19. Thallus slightly granulose, disappearing 21
20. Ascospores 7–8 × 3–4 μ; Uganda ..... *L. Cagnii* Jatta
20. Ascospores 9.5–15 × 5.5–6 μ; Ruanda ..... *L. argillicola* Lindau
21. Apothecia white-pruinose when young, then black; ascospore size not given; Abyssinia ..... *L. bogosensis* Zahlbr.
21. Apothecia black, 0.5–0.7 mm.; ascospores 8–11 × 2.5–3 μ; Angola ..... *L. leptobola* Nyl.

Lecidea granifera Vainio, Cat. Welwitsch Afric. Pl. 2:424. 1901.

Lecanora granifera Ach., Syn. Lich. 164. 1814.

Type: Guinea, corticole, Afzelius.

Thallus crustose, verrucose, 100–125 μ thick, vetiver green; cortex 10–12 μ

thick, gelified, amorphous; algae *Trebouxia,* cells subspherical, 5–6 μ in diameter, closely packed in spherical colonies about 20 μ in diameter; medulla of thick-walled hyphae 7–8 μ in diameter, very loosely woven in the larger warts; cortex finally disappearing and the colonies of algae escaping as soredia, not in definite soralia. Apothecia biatorine, round at first, becoming very irregular, sublobate from unequal expansion of the parathecium, margin white, disc benzo brown to fuscous, slightly pruinose when young, partly immersed to sessile on thalline warts, the thallus extending nearly to the top of the parathecium when young, forming a thin pseudo-amphithecium, but covering only the base of the parathecium when mature; parathecium hyaline, 370 μ thick in the center, thinning to the slightly elevated margin, slightly inflexed when dry and disc slightly concave to plane, when moist the parathecium is almost level with the slightly convex disc, composed of radiating pseudoparenchyma, highly gelified, the upper 40 μ under the hypothecium fuliginous, the rest hyaline; thecium 95 μ tall; hypothecium not clearly differentiated; paraphyses conglutinate, slender, once or twice dichotomous above the asci, tips not thickened in the slightly brownish epithecial gel; asci 8-spored, clavate, tip thickened when young, 55 $\times$ 8 μ; ascospores unicellular, monostichous, subspherical, 7–8 μ in diameter.

Due to the deep fuliginous color which extends from the upper part of the parathecium through the hypothecium shading off gradually through the lower 25 μ of the thecium, it is very difficult to see how much is hypothecium and its structure. The systematic position of this species is somewhat uncertain. In the young stages, the sides of the parathecium are nearly covered by thallus and very rarely one can find an algal cell which has penetrated the outer side of the parathecium, so that one might be justified in following Acharius and leaving the species in *Lecanora.* On the other hand, the very highly developed, biatorine parathecium and lack of algal layer or medulla of an amphithecium in the mature apothecium suggest a much closer relation to *Lecidea* sect. *Biatora* where it was placed by Vainio. This is a very different situation from the ambiguous species between *Rinodina* and *Buellia* where a true amphithecium is formed, then the algae die and the amphithecium blackens but leaves traces of medulla and lacunae where the algae have disappeared. Vainio recognized two varieties: *lecanoroides,* the typical form, and *leucotropoides,* with a testaceous disc, which he later raised to specific rank. I have seen no material referable to the latter.

Nigeria: Ina near Ibadan, on *Theobroma,* C. A. Thorold 151a *pro parte,* 156; Ondo Province, Owena and Aponmu near Akure on *Theobroma,* C. A. Thorold 157, 158, respectively.

LECIDEA TENUIS Müll. Arg., Linnaea 63:34. 1880.

Type: Angola, Quillu River, growing over sterile *Chiodecton,* Pechuel-Loesche.

Thallus smooth to minutely verrucose, deep olive buff, not black-margined, 80 μ thick; cortex 6–8 μ thick, decomposed, of periclinal hyphae; algae *Trebouxia?,* in discrete cylindric colonies 25–40 μ in diameter, cells 4–8 μ in diameter; medulla

scarcely differentiated. Apothecia 0.4–0.5 mm. in diameter, margin white, disc waxy, plane at first, becoming very convex, warm buff; parathecium 180 μ thick below the hypothecium, thinning to 40 μ or less at the top of the thecium, hyaline, the inner 100 μ of gelified, thick-walled, periclinal hyphae, the outer 80 μ of radiating, septate hyphae 6 μ in diameter, forming a pseudoparenchyma; hypothecium 30 μ thick, of slender, more deeply staining, vertical hyphae, not sharply differentiated from the thecium; thecium 40 μ tall; paraphyses slender, once or twice dichotomous above the asci, tips not thickened in the very pale brownish epithecial gel; asci cylindric-clavate, 8-spored, 30 $\times$ 6 μ; ascospores hyaline, unicellular, long-ellipsoid, thin-walled, 6–7 $\times$ 2–3 μ.

Our material differs in some respects from Müller Argau's description. The apothecia are more strongly convex at maturity, the parathecium (hypothecium of Müller Argau) is not slightly yellowish below, and the ascospores are slightly shorter and broader (Müller Argau states: 8–11 $\times$ 2–2.5 μ). *L. microspermoides* Müll. Arg., from Usambara, has a chalky thallus, larger apothecia, a darker disc and ascospores 7–9 $\times$ 2–3 μ.

Nigeria: Ondo, on *Theobroma*, C. A. Thorold 110.

Lecidea (Biatora) **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Ekialodor near Benin City, on *Theobroma*, C. A. Thorold 135.

Thallus epiphloeodes, laevis vel subrugulosus, nigro-marginatus, obscure olivaceo-alutaceus, 80 μ crassitudine; cortex vix evolutus; algae protococcoideae, cellulis 6–8 μ diametro; medulla nulla. Apothecia 0.5–0.6 mm. diametro, margine thallo concolore, disco plano, subpruinoso, brunneo, linea angusta nigra circumdato; parathecium hyalinum, 110–120 μ crassitudine sub hypothecio, superne ad 40 μ tenuescens, pseudoparenchymaticum, cellulis 5–8 μ diametro, radialiter elongatis; hypothecium 20 μ crassitudine, hyphis subbrunneis, dense contextum; thecium 95 μ altitudine; paraphyses tenues, semel bisve dichotome ramosae super ascos, apicibus non incrassatis; asci clavati, 80 $\times$ 8 μ; ascosporae octonae, inbricatim monostichae vel subdistichae, hyalinae, ellipsoideae, uniloculares (false biloculares juventute), 8–11 $\times$ 4–5.5 μ.

Thallus smooth to slightly wrinkled, black-margined, deep olive buff, 80 μ thick; cortex not differentiated; algae protococcoid, cells 6–8 μ in diameter, filling the whole thallus but more densely packed above. Apothecia 0.5–0.6 mm. in diameter, margin concolorous with the thallus, disc plane, slightly pruinose, buckthorn brown, surrounded by a very narrow black line due to blackening of the top of the parathecium next the thecium; parathecium hyaline, 110–120 μ thick below the hypothecium, thinning to 40 μ at the top of the thecium, pseudoparenchymatous, cells 5–8 μ in diameter, elongated radially; hypothecium 20 μ thick, of densely woven, slightly brownish hyphae; thecium 95 μ tall; paraphyses slender, once or twice dichotomous above the asci, tips not enlarged in the very pale brownish epithecial gel; asci clavate, 8-spored, 80 $\times$ 8 μ; ascospores imbricately monostichous to subdistichous, hyaline, ellipsoidal, unilocular (falsely bilocular when young), 8–11 $\times$ 4–5.5 μ.

LECIDEA RUBINA Ach., Syn. Lich. 40. 1814.

Biatora rubina Bél., Voy. Ind. Orient. 2:Crypt.:128. 1846.

Type: Guinea, on bark of *Uvaria* etc., Afzelius.

Thallus smooth, somewhat rimose, citrine drab, 55 μ thick; cortex 8 μ thick, decomposed, of periclinal hyphae; algal layer 20–25 μ thick, of rounded colonies of *Trebouxia,* cells about 5 μ in diameter, closely packed; medulla of densely woven, subvertical hyphae, penetrating between the cork cells and disorganizing them to a depth of 40 μ. Apothecia 0.7–1 mm., round, sessile, margin concolorous with the thallus, disc plane then convex, isabelline, darkening; parathecium 105 μ below the hypothecium, thinning to 55 μ at the level of the thecium, the inner half deep fuliginous, the outer half hyaline, of thick-walled pseudoparenchyma, cells 5–6 μ in diameter, elongated radially; hypothecium about 15 μ thick, not sharply differentiated; thecium 95 μ tall; paraphyses coherent, gelified, once or twice dichotomous above the asci, ending in the slightly brownish epithecial gel; asci clavate, 8-spored, 65 $\times$ 12 μ, wall and tip thickened when young; ascospores imbricately monostichous to subdistichous, hyaline, unilocular, ellipsoidal, 11–12 $\times$ 5–6 μ.

After the ascospores are shed, new apothecia proliferate from the margins of the disc and become partly confluent, resulting in lobed and distorted apothecia. *Thorold 131* has the fuliginous portion of the parathecium 135 μ thick in the center and the hyaline portion 55 μ, otherwise it is similar to the other specimens.

Nigeria: Ife near Ibadan, on *Theobroma,* C. A. Thorold 152; Ondo Province, Aponmu near Akure, on *Theobroma,* C. A. Thorold 153; Igede near Ado Ekiti, on *Theobroma,* C. A. Thorold 154; Ondo, on *Theobroma,* C. A. Thorold 109; Ado Ekiti near Ondo, on *Theobroma,* C. A. Thorold 131.

BACIDIA

BACIDIA DNtrs., Giorn. Bot. Ital. 1:189. 1846.

Type: Not designated, based on *Lecidea rosella* Ach. and *L. carnea* Ach. Since *L. carnea* Ach. has been transferred elsewhere, we may accept *L. rosella* Ach. as the type, as this would conserve the genus in its sense commonly used. The synonymy of this very large and variable genus is very confused, hence I have not cited the various synonyms. In our collections there are only two species, one in sect. *Weitenwebera* Zahlbr. (*Bilimbia* DNtrs. *non* Reichb., *Weitenwebera* Opiz *non* Schrank) with fusiform ascospores, and one in sect. *Eubacidia* Zahlbr. with acicular ascospores. As these two sections are well represented in tropical Africa, I have prepared keys.

Thallus crustose, homoeomerous or heteromerous; ecorticate or cortex poorly developed; algae protococcoid. Apothecia sessile, rarely somewhat immersed or almost stipitate, with a flat or very convex disc; parathecium light-colored; hypothecium hyaline or darkening; asci usually 8-spored; ascospores hyaline, long-fusiform to acicular, 3–many-septate, walls and septa thin, protoplasts cylindric, straight, curved, or helical. Spermatia exobasidial, acicular, straight or curved.

1. Ascospores long-ellipsoid to fusiform, not over 25 μ long; sect. Weitenwebera (Bilimbia DNtrs. et Auct.) 2
1. Ascospores acicular, over 25 μ long, usually not over 3 μ in diameter; sect. Eubacidia 10
2. Ascospores more than 14 μ long, 4–8-locular 3
2. Ascospores less than 14 μ long, 4-locular 7
3. Apothecia yellowish testaceous, ascospores 4-locular, 14–17 × 4–5 μ; São Thomé ..... *Catillaria subternella* (Nyl.) Zahlbr.
3. Apothecia finally black or nearly so 4
4. Ascospores 4-locular, 14–17 × 4–5 μ 5
4. Ascospores 6–8-locular, 17–22 μ long 6
5. Thallus white, disc black; São Thomé ..... *B. imitans* (Nyl.) Zahlbr.
5. Thallus ashy white, disc olive black; Usambara ..... *B. stellaris* (Müll. Arg.) Zahlbr.
6. Hypothecium hyaline; ascospores 17–22 × 5–6 μ, disc fuscous; Abyssinia ..... *B. abessinica* (Müll. Arg.) Zahlbr.
6. Hypothecium fuscous; ascospores 18 × 3 μ; disc black; Uganda ..... *B. Scottii* (Vainio) Zahlbr.
7. Thallus white, somewhat farinaceous 8
7. Thallus yellowish 9
7. Thallus green; apothecia 0.15–0.25 mm., disc fuscous; Angola ..... *B. exiguella* (Vainio) Zahlbr.
8. Apothecia black, ascospores 10–12 × 3.5 μ; São Thomé ..... *B. vagula* (Nyl.) Zahlbr.
8. Apothecia rose fleshcolor; ascospores 8–12 × 2.5–3.5 μ; Angola ..... *B. farinulenta* (Müll. Arg.) Zahlbr.
9. Thallus yellowish ashy; apothecia 0.3–0.5 mm., disc and hypothecium fuscous; Angola ..... *B. sublecanorina* (Müll. Arg.) Zahlbr.
9. Thallus pale yellow-olive; apothecia 0.5–0.8 mm., disc ochraceous orange; hypothecium hyaline; Nigeria ..... *B. nigeriensis* Dodge
10. Disc white-pruinose, epithecium and hypothecium fuscous; ascospores 27–34 × 5–5.5 μ, 6–8-locular; Central Africa ..... *B. griseoalba* Lindau
10. Disc flesh color to rufous, at least when young 11
10. Disc soon black 14
11. Hypothecium rufous becoming fuscous; ascospores 62–70 × 2–4 μ; Kenya ..... *B. araneosa* (Hue) Zahlbr.
11. Hypothecium deep yellow; ascospores 40–65 × 2.5–3 μ, 8–10-locular; Kenya ..... *B. submillegrana* Steiner
11. Hypothecium hyaline (sometimes slightly yellowish in *B. nigrocincta*) 12
12. Ascospores 45–55 × 3.5–4.5 μ; apothecia 0.5–1 mm., disc flesh color; hypothallus black; Usambara ..... *B. nigrocincta* (Müll. Arg.) Zahlbr.
12. Ascospores less than 42 μ long 13
13. Ascospores 25–30 × 1.5 μ; apothecia 0.4–0.6 mm.; thallus ashy olive; Usambara ..... *B. trichosperma* (Müll. Arg.) Zahlbr.
13. Ascospores 28–32 × 2.5 μ; apothecia 0.25–0.4 mm.; thallus white; Ascension Island ..... *B. atlantica* (Müll. Arg.) Zahlbr.
13. Ascospores 26–42 × 2.5–3 μ; apothecia 0.5 mm.; thallus glaucous; Angola ..... *B. golungensis* (Vainio) Zahlbr.
13. Ascospores 38–41 × 4 μ; thallus ochraceous; Abyssinia ..... *B. Kotschyi* (Krmphbr.) Zahlbr.
14. Hypothecium tawny fuscous to rufous; thallus white or glaucescent 15
14. Hypothecium deep yellow; thecium 75–80 μ; ascospores 72–80 × 3 μ, 15–20-locular; Usambara ..... *B. endoleucella* v. *colorata* Zahlbr.
14. Hypothecium hyaline 16
15. Ascospores 34–38 × 2–2.5 μ, 4–6-locular; apothecia 0.7–1 mm.; Guinea (Togoland) ..... *B. infuscata* (Müll. Arg.) Zahlbr.
15. Ascospores 42–58 × 3.5–4 μ, 8–9-locular; apothecia 0.8–1 mm.; Angola ..... *B. byssothallina* (Vainio) Zahlbr.
15. Ascospores 62 × 3–3.5 μ, 10–14-locular; apothecia 0.5–1 mm.; Socotra ..... *B. socotrana* (Müll. Arg.) Zahlbr.
15. Ascospores 55 × 4 μ, 10–15-locular; apothecia 0.3–0.4 mm.; Socotra ..... *B. decussata* (Müll. Arg.) Zahlbr.
16. Ascospores 46–54 × 2–3 μ; Angola ..... *B. amylothelia* Vainio
16. Ascospores 65–75 × 3–4 μ; São Thomé ..... *B. leucotrypta* (Nyl.) Zahlbr.
16. Ascospores 36–56 × 2–3.5 μ, 6–10-locular; Angola ..... *B. heteroloma* v. *elongata* (Vainio) Zahlbr.
16. Ascospores 17–28 × 3.5 μ; thecium 55–60 μ; Angola ..... *B. heteroloma* v. *bacteriospora* (Vainio) Zahlbr.

BACIDIA (WEITENWEBERA) **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Ondo Province, Owena, on *Theobroma,* C. A. Thorold 111.

Thallus laevis vel minute verruculosus, pallide flavo-olivaceus, 40–80 μ crassitudine; cortex vix evolutus; stratum algarum 25 μ crassitudine, cellulis protococcoideis 5–6 μ diametro; medulla 15–55 μ crassitudine, hyphis 3 μ diametro, laxe intertextis. Apothecia sessilia, 0.5–0.8 mm. diametro, margine albo, disco ceraceo, ochraceo-aurantiaco, madefacto albo; parathecium hyalinum, inferne 55 μ crassitudine, superne ad 25 μ tenuescens, pseudoparenchymaticum, dimidia parte exteriore hyphis radiantibus 5–6 μ diametro, cellulis terminalibus rotundatis majoribusque, dimidia parte interiore hyphis periclinalibus 3–4 μ diametro; hypothecium ca. 15 μ crassitudine; thecium 55 μ altitudine; paraphyses tenues, liberae, 2.5 μ diametro, pachydermeae, apicibus non incrassatis; asci clavati, 30 $\times$ 6 μ; ascosporae octonae, ellipsoideae vel subfusiformes, hyalinae, leptodermeae, 4-loculares, 9–12 $\times$ 2.5–3 μ.

Thallus smooth to minutely verrucose, 40–80 μ thick, light yellowish olive; cortex not well differentiated; algal layer 25 μ thick, protococcoid cells 5–6 μ in diameter, in a compact layer; medulla 15–55 μ thick, of loosely woven hyphae about 3 μ in diameter. Apothecia sessile, 0.5–0.8 mm. in diameter, margin white, disc waxy, ochraceous orange becoming almost white when moistened; parathecium hyaline, 55 μ thick below the hypothecium, thinning to 25 μ thick above, pseudoparenchymatous, the outer half of radiating hyphae 5–6 μ in diameter, outermost cells rounded and somewhat larger, inner half of mostly periclinal hyphae 3–4 μ in diameter; hypothecium about 15 μ thick, not sharply differentiated; thecium 55 μ tall; paraphyses slender, free, about 2.5 μ in diameter, thick-walled, tips not thickened; asci clavate, 8-spored, about 30 $\times$ 6 μ, tips somewhat thickened when young; ascospores ellipsoid to subfusiform, hyaline, 4-locular, thin-walled, 9–12 $\times$ 2.5–3 μ.

It is with some hesitation that I have referred *Deighton M4307A* to this species, as the parathecium is 95–105 μ thick below, thinning to 55 μ above, and the ascospores are smaller, 7–9 $\times$ 2.5–3 μ; otherwise it agrees well with the Nigerian material.

Nigeria: Ondo Province, Owena, on *Theobroma,* C. A. Thorold 111, type; Ikere near Ondo, on *Theobroma,* C. A. Thorold 112.

Sierra Leone: Njala (Kori), on twigs of *Bauhinia tomentosa,* F. C. Deighton M4307A.

BACIDIA (EUBACIDIA) GOLUNGENSIS (Vainio) Zahlbr., Cat. Lich. Univ. 4:202. 1926.

Lecidea golungensis Vainio, Cat. Welwitsch Afric. Pl. 2:419. 1901.

Type: Angola, Golungo Alto, near Sange, 320–775 m., Welwitsch 135a, 136 as v. *pauciseptata,* 149 *p.p.* as v. *pluriseptata;* Serra de Alta Queta, Welwitsch 150c, 151 as v. *pauciseptata,* 154 as v. *pluriseptata.* No specimen cited as type of the species (see discussion below).

Thallus granular-verrucose, continuous, citrine drab, 40 μ thick; cortex gelified, 5–6 μ thick; algal colonies discrete, 15–20 μ in diameter, of *Trebouxia,* closely packed cells 3–4 μ in diameter; medulla 14–19 μ thick, gelified, of densely woven hyphae. Apothecia sessile, margin very thin, soon immarginate, 0.5 mm. in diameter, sometimes concrescent in groups up to 1 mm. in diameter, disc avellaneous to wood brown; parathecium 80–150 μ thick below the hypothecium, thinning to 25 μ at the top of the thecium, hyaline, inner half of slender, periclinal gelified hyphae, the outer half of radiating, thick-walled, conglutinate hyphae 5–6 μ in diameter, occasionally penetrated by a few algal cells; hypothecium 15 μ thick, of densely woven, mostly periclinal, slender hyphae; thecium 55–70 μ tall; paraphyses slender, coherent, once or twice dichotomous above the asci, tips clavate in the slightly brownish epithecial gel; asci cylindric-clavate, 8-spored, about 45 $\times$ 8 μ; ascospores acicular, fascicled, 3–6-septate, 26–42 $\times$ 2.5–3 μ. Spermogonia spherical, half emersed from the thallus at the edge of the parathecium, about 80 μ in diameter, wall of exposed portion blackened to a depth of 15 μ, rest hyaline, filamentous, 15 μ thick; spermatiophores flask-shaped, about 10 $\times$ 2 μ; spermatia bacilliform, straight, about 6 $\times$ 1 μ.

Vainio separated this species into two varieties, *pauciseptata,* with the thecium 55–65 μ tall, ascospores 4-locular, 26–36 μ long, and var. *puriseptata,* with the thecium 60–70 μ tall, ascospores 5–7-locular, 38–42 μ long. In my material, using gentle pressure on the cover glass, I have found free ascospores 32 and 40 μ long up to 8-locular.

Nigeria: Ina near Ibadan, on *Theobroma,* C. A. Thorold 151; Ondo Province, Aponmu near Akure, on *Theobroma,* C. A. Thorold 172b.

Bacidia heteroloma Zahlbr., Cat. Lich. Univ. 4:204. 1926.

Lecidea heteroloma Vainio, Cat. Welwitsch Afric. Pl. 2:418. 1901.

Type: Angola, Golungo Alto, near Sange, 360–775 m., corticole, Welwitsch 125, 148, 149.

Thallus slightly verrucose, uneven and rimose, margin pale, indefinite on bark, pale olive buff, 65–80 μ thick; cortex 10–12 μ thick, of slender thin-walled periclinal hyphae, the outer ones somewhat decomposed; algae *Trebouxia,* filling the rest of the thallus, cells about 6 μ in diameter; medullary hyphae partly disintegrating bark cells to a depth of 140 μ. Apothecia sessile, constricted at the base, round or somewhat distorted by mutual pressure, 0.5–0.7 mm. in diameter or in groups 1 $\times$ 2 mm.; margin prominent, pale ashy or brownish becoming nearly black in age, disc concave to plane, fuscous black; parathecium sulphate green when first sectioned soon fading in lacto-phenol, 140 μ thick below the hypothecium, thinning to 65 μ at the top of the thecium, of radiating pseudoparenchyma, cells 6–8 μ in diameter, thick-walled; hypothecium probably hyaline (pale brown in my moribund specimens), about 25 μ thick, of closely woven, slender

hyphae; thecium 60 μ tall; paraphyses slender, dichotomous above the asci, tips not thickened in the pale brownish epithecial gel; asci long-ellipsoid, 8-spored, 45 $\times$ 6 μ; ascospores hyaline, acicular, plurilocular, 35 $\times$ 2.5 μ.

My material is moribund, and much of the thecium has begun to disintegrate. The one ascus near the parathecium clearly seen is probably somewhat immature, as I could not see the septa of the ascospores clearly enough to count them and I found no free ascospores. Vainio describes the ascospores as 36–56 $\times$ 2–3.5 μ, 6–10-locular. He described two varieties: v. *elongata* which should be taken as his *varietas typica* since he repeats the dimensions of the ascospores for it, and v. *bacteriospora* with paler apothecial margins and smaller ascospores 17–28 $\times$ 3–3.5 μ.

Sierra Leone: Njala (Kori), on *Phyllanthus discoideus*, F. C. Deighton M4581.

LOPADIUM

LOPADIUM Koerb., Syst. Lich. Germ. 210. 1854.

Heterothecium Mont. in Gay, Hist. Fís. Polít. Chile, Bot. 8:175. 1852, *non* Flotow, 1850.

Brigantiaea Trev., Spighe e Paglie 7. 1853.

Type: *L. pezizoideum* (Ach.) Koerb. *Heterothecium* Mont., *non* Fw., was based on *H. Berteroanum* Mont. *Brigantiaea* Trev. was based on *Heterothecium Berteroanum* Mont., *B. Mariae* Trev., *B. tricolor* Trev., *B. tristis* Trev., and *B. argentea* Trev. When *Lopadium sensu latiore* is monographed, it seems probable that *Brigantiaea* Trev. will be recognized as a separate genus, and there will be no need to conserve *Lopadium* Koerb.

Thallus crustose, ecorticate or nearly so; algae protococcoid. Apothecia sessile; parathecium fleshy, cartilaginous, and light colored, or carbonaceous; hypothecium hyaline to dark colored; asci 1–8-spored; ascospores hyaline, muriform, thin-walled, without a halo; spermatia ellipsoidal, short, straight.

1. Foliicolous 2
1. Corticolous; asci monosporous, rarely 2–3-spored 3
   2. Asci 8-spored; ascospores 18–19 $\times$ 8–9 μ, 4(–7)-locular, 2(–4)-locellate, disc black; São Thomé ..... *L. Newtonianum* (Henriques) Sant.
   2. Asci 1-spored; ascospores 65–85 $\times$ 16–23 μ, disc fuscescent, flesh color; São Thomé; ..... *L. glaucophaeoides* (Nyl.) Zahlbr.
3. Thallus white 4
3. Thallus glaucous; disc testaceo-fuscous, margin pale; ascospores 60–73 $\times$ 20–24 μ; Angola ..... *Lecidea olivacea* v. *alsodinea* Vainio
3. Thallus olive buff or darker 5
   4. Disc watery fuscous, margin with thalline granules; ascospores 65 $\times$ 25 μ; Usambara ..... *L. lecanorinum* Müll. Arg.
   4. Disc sepia, only slightly pruinose; ascospores 32–43(–60) $\times$ 19–21 μ; Sierra Leone ..... *L. sepiaceum* Dodge
5. Disc isabelline, coarsely white-pruinose; ascospores 61–88 $\times$ 16–20 μ; Sierra Leone ..... *L. Deightoni* Dodge
5. Disc and margin clove brown, blackening; ascospores 43–56(–66) $\times$ 16–21(–23) μ; Sierra Leone ..... *L. nigrobrunneum* Dodge

LOPADIUM sepiaceum Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Bauhinia tomentosa*, F. C. Deighton M4307B.

Thallus verruculosus, margine pallido, 80 μ crassitudine, albidus; cortex vix evolutus; algae protococcoideae, cellulis 5–6 μ diametro. Apothecia sessilia, basi constricta, margine subelevata, thallo concolore, subpruinosa, disco sepiaceo; parathecium inferne 55 μ, superne ad 15 μ tenuescens, hyphis pachydermeis radiantibus, luminibus 4 μ diametro, hyalinum, extus brunnescens; hypothecium brunneum, centro 55 μ ad marginem 15 μ tenuescens, hyphis 4–5 μ diametro; thecium 105–110 μ altitudine; paraphyses super ascos dichotome ramosae, apicibus non incrassatis; asci pachydermei, cylindrici, 95 $\times$ 20–24 μ; ascosporae binae vel ternae, muriformes, pallide brunneae, ellipsoideae, 32–43 (–60) $\times$ 19–21 μ.

Thallus whitish, minutely verrucose, margin pale, 80 μ thick; cortex not well differentiated; algae protococcoid, filling the whole thallus, but not closely packed, cells 5–6 μ in diameter. Apothecia sessile, constricted at the base, margin slightly elevated, concolorous with the thallus, slightly pruinose, disc sepia; parathecium 55 μ thick below, thinning to 15 μ above, of thick-walled radiating hyphae, lumen about 4 μ in diameter, hyaline, brownish on the outside; hypothecium deep brown, 55 μ thick in the center, thinning to 15 μ at the margin, of hyphae 4–5 μ in diameter; thecium 105–110 μ tall; paraphyses dichotomous above the asci, tips not thickened in the brown epithecial gel; asci thick-walled, cylindric, 2–3-spored, 95 $\times$ 20–24 μ; ascospores monostichous, muriform, pale brownish, without a halo, ellipsoid, 32–43 (–60) $\times$ 19–21 μ.

LOPADIUM **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Bauhinia tomentosa,* F. C. Deighton M4307C.

Thallus minute verruculosus, margine pallido, 65 μ crassitudine, obscure olivaceo-alutaceus; cortex vix evolutus, ca. 8 μ crassitudine, hyphis periclinalibus; stratum algarum 25 μ crassitudine, continuum, cellulis protococcoideis, 5–6 μ diametro, laxe dispositis; medulla 30–35 μ crassitudine, hyphis dense contexta. Apothecia 0.6–0.8 mm. diametro, basi constricta, margine subelevato, disco concolore, pruinoso; discus isabellinus, planus, granuloso-pruinosus; parathecium inferne 65 μ crassitudine, superne ad 30 μ tenuescens, hyalinum, pseudoparenchymaticum, cellulis radiantibus; hypothecium centro 40 μ crassitudine, ad marginem 15 μ tenuescens, hyphis periclinalibus dense contextum; thecium 130 μ altitudine, superficie inaequali; paraphyses pachydermeae, super ascos dichotome ramosae, cellula apicali subsphaerica, 5–6 μ diametro; asci cylindrico-clavati, pachydermei, 120 $\times$ 27 μ; ascosporae solitariae vel rare binae, ellipsoideae, hyalinae vel subbrunneae, sine halone, muriformes, 61–88 $\times$ 16–20 μ (solitariae) vel 50–60 $\times$ 16 μ (binae).

Thallus minutely verruculose, margin pale, 65 μ thick, deep olive buff; cortex scarcely developed, about 8 μ thick, of periclinal hyphae; algal layer continuous, protococcoid, cells 5–6 μ in diameter, loosely packed; medulla 30–35 μ thick, of densely woven hyphae. Apothecia 0.6–0.8 mm. in diameter, constricted at the base, margin somewhat elevated, pruinose, colored like the disc which is plane, isabelline, covered by a coarse granular pruina; parathecium 65 μ thick below,

thinning to 30 μ above, hyaline, pseudoparenchymatous, cells radiating; hypothecium 40 μ thick in the center, of closely woven, periclinal hyphae; thecium 130 μ tall, surface uneven; paraphyses thick-walled, dichotomously branched above the asci, the terminal cells subspherical, 5–6 μ in diameter; asci cylindric-clavate, thick-walled, 1–2-spored, 120 $\times$ 27 μ; ascospores ellipsoid, hyaline or slightly brownish when old but without a halo, muriform, 61–88 $\times$ 16–20 μ when single, 50–60 $\times$ 16 μ when two per ascus.

Deighton 4344 is older than the type and the apothecia have begun to disintegrate, but the structure is the same and the spores are of the same size. The thallus bears abundant campylidia, otiform, conchiform or cyphelliform, cinnamon buff, about 1 mm. tall and broad; stalk 125 μ tall, 250 μ in diameter with hairs 40 μ long; context 120–135 μ thick, the outer 15 μ forming a fine tomentum of curved, brownish, thick-walled hairs 5–6 μ in diameter, with protococcoid algae penetrating in an irregular layer 80–90 μ thick, the rest of conglutinate, densely woven, thick-walled, hyaline hyphae 6 μ in diameter; subhymenium about 15 μ thick, of slender vertical hyphae covering the inner (proximal) portion, leaving the distal portion of the cup sterile; conidiophores somewhat flexuous, 30 $\times$ 3 μ, with 1–2 short sterigmata; conidia 16 $\times$ 2 μ, very thin-walled, slightly curved, unicellular.

The campylidium has often been considered a parasitic fungus and described as a species of *Cyphella* or *Chlorocyphella*, but the layer of protococcoid algae is similar to those of the species of *Lopadium* on which it develops, and continuous with the algal layer of the thallus. This seems to indicate that it is a genuine conidial state of the fungus component of *Lopadium*, as originally described by Müller Argau. Frequently I have seen this conidial state on various species of *Lopadium* and on the foliicolous *Sporopodium* from Texas southward in tropical America.

Sierra Leone: Njala (Kori), on *Bauhinia tomentosa*, F. C. Deighton M4307C, type; on *Lagerstroemia speciosa*, F. C. Deighton M4344.

LOPADIUM **nigrobrunneum** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on twigs of *Lagerstroemia speciosa*, F. C. Deighton M4346.

Thallus verruculosus subrimulosusque, in hypothallo nigro, 65 μ crassitudine, olivaceo-alutaceus; cortex vix evolutus; stratum algarum 20–25 μ crassitudine, protococcoideum, cellulis 6–7 μ diametro; medulla 25–30 μ crassitudine, hyphis 3–4 μ diametro laxe intertextis; hypothallus 15 μ crassitudine hyphis periclinalibus brunneis. Apothecia 0.5–0.7 mm. diametro, subconvexa, basi constricta, margine et disco nigricantibus; parathecium inferne 40 μ crassitudine, superne ad 15 μ tenuescens, pseudoparenchymaticum, hyalinum, hyphis radiantibus, cellulis 6–7 μ diametro; hypothecium obscure brunneum, centro 40 μ crassitudine ad marginem 20 μ tenuescens; thecium 100–105 μ altitudine, superficie inaequali; paraphyses conglutinatae, pachydermeae, super ascos dichotome ramosae, apicibus non in-

crassatis; asci cylindrico-clavati, ca. 100 × 30 μ; ascosporae solitariae vel binae, hyalinae vel subbrunneae, sine halone, muriformes, 43–56(–66) × 16–21(–23) μ.

Thallus minutely verrucose and subrimulose, on a black hypothallus, olive buff, 65 μ thick; cortex scarcely differentiated; algal layer 20–25 μ thick, protococcoid, cells 6–7 μ in diameter; medulla 25–30 μ thick, of somewhat loosely woven hyphae 3–4 μ in diameter; hypothallus 15 μ thick, of periclinal brown hyphae. Apothecia 0.5–0.7 mm. in diameter, slightly convex, constricted at the base, margin and disc clove brown, blackening; parathecium 40 μ thick below, thinning to 15 μ at the slightly inflexed top, pseudoparenchymatous, of radiating hyphae, cells 6–7 μ in diameter; hypothecium very dark brown, 40 μ thick in the center, thinning to 20 μ at the margin; thecium 100–105 μ tall, surface very uneven; paraphyses conglutinate, thick-walled, dichotomous above the asci, tips not enlarged in the brownish, epithecial gel, filled with minute granules; asci 1(–2)-spored, cylindric-clavate, about 100 × 30 μ; ascospores hyaline to slightly brownish, without a halo, muriform, 43–56(–66) × 16–21(–23) μ.

PHYLLOPSORACEAE

Thallus squamulose to subfoliose, often somewhat erect, attached to the substrate by rhizinae; upper cortex well developed; algae protococcoid. Apothecia rounded, sessile; amphithecium absent, parathecium light or dark; paraphyses unbranched; ascospores hyaline, unilocular or septate.

Although there is no clear differentiation of primary thallus and podetia which one finds in the Cladoniaceae, this family seems much closer to it than to the Lecideaceae. Only two genera are known: *Phyllopsora* with unilocular ascospores, and *Psorella* with 4–16-locular ascospores. Our material belongs in the former genus.

PHYLLOPSORA

PHYLLOPSORA Müll. Arg., Bull. Herb. Boissier 2:append. 1:11, 45. 1894.
?*Psoromidium* Stirton, Proc. Phil. Soc. Glasgow 10:304. 1877.

Type: not designated but *P. parvifolia* (Pers.) Müll. Arg., one of the best-known species, may be chosen. *Psoromidium* Stirton was based on *P. Wellingtonii* Stirton.

Characters of the family: ascospores unilocular, long-ellipsoid, hyaline.

1. Squamules not long white-ciliate; fertile 2
1. Squamules long, snowy-white ciliate, upper surface pale yellowish; sterile; Usambara..... *P. pannosa* Müll. Arg.
   2. Ascospores very long-ellipsoid, 10–12 × 2.5–3.5 μ; Togoland..... *P. Buettneri* (Müll. Arg.) Zahlbr.
   2. Ascospores relatively short ellipsoid, 5–7.5 × 3.5–5 μ; Usambara..... *P. brachyspora* Müll. Arg.

PHYLLOPSORA BUETTNERI Zahlbr., Cat. Lich. Univ. 4:396. 1926.

Psora Buettneri Müll. Arg., Bot. Jahrb. [Engler] 15:506. 1893.
Lecidea Buettneri Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 1893/4:246. 1895.

Type: Togoland, Bismarcksburg, corticole, R. Buettner.

Hypothallus fuscous black, almost completely covered by light yellowish olive squamules, imbricate, less than 1 mm. broad, deeply lobed, the lobes becoming erect isidia, so that the whole thallus appears isidiose and minutely granular-sorediose. Apothecia convex, immarginate, constricted below into a substipitate base, 0.35 mm. broad, 0.25 mm. tall, disc cinnamon rufous; parathecium of hyaline, thick-walled, densely woven hyphae 3–4 μ in diameter, containing a few small colonies of *Trebouxia* cells 6–8 μ in diameter; hypothecium 70 μ thick, of thick-walled, vertical hyphae, very dark brown next the thecium, shading to hyaline next the base; thecium 25 μ tall; paraphyses conglutinate, tips not thickened, somewhat dichotomous in the upper portion; asci cylindric, 8-spored, about 20 $\times$ 8 μ; ascospores fascicled, unicellular, long-ellipsoid, 10–12 $\times$ 2.5–3.5 μ.

Some ascospores contain 3–5 large oil droplets, when the ascospores appear 3–5-septate and might lead one to look for the species in *Psorella*.

Gold Coast: Tafo, West African Research Institute, on *Theobroma*, C. A. Thorold 155.

Nigeria: Ondo Province, Aponmu near Akure, on *Theobroma*, C. A. Thorold 173.

Lecanoraceae

Thallus crustose, uniform or with effigurate margins, rarely dwarf-fruticose, branched, attached to the substrate by hyphae of the hypothallus or of the medulla, without rhizinae; heteromerous (except in *Harpidium*); ecorticate or corticate; algae *Protococcus* or *Trebouxia*. Apothecia immersed in the thallus, to sessile, round; amphithecium well developed; parathecium very poorly developed or lacking; hypothecium hyaline or brownish, usually with algae below it; paraphyses unbranched (except in *Ochrolechia* and *Phlyctidia*); asci 8–32-spored; ascospores hyaline (brownish in some species of *Myxodictyon*), unilocular, septate or muriform.

1. Thallus homoeomerous, pseudoparenchymatous; ascospores sickle-shaped; known only from Europe ..... *Harpidium* Koerb.
1. Thallus heteromerous, plectenchymatous 2
2. Ascospores unilocular 5
2. Ascospores bilocular 8
2. Ascospores 4–pluri-locular 10
2. Ascospores muriform 4
3. Paraphyses unbranched or sparingly dichotomous above the asci ..... *Ochrolechia* Mass.
3. Paraphyses branched, sparse in the thecial gel; ascospores large but relatively thin-walled [perhaps belongs in the Pertusariaceae] ..... *Lecanora* Ach.
4. Thallus not bright yellow to orange; spermatia acicular, straight or curved ..... *Candelariella* Müll. Arg.
4. Thallus bright yellow or orange; spermatia ellipsoidal, straight 6
5. Ascospores ellipsoid to subcylindric; spermatiophores unbranched, spermatia terminal 7
5. Ascospores fusiform; spermatiophores branched, septate, spermatia lateral ..... *Lecania* Mass.
6. Thallus gray or brown; spermatia straight or curved, acicular ..... *Candelariella* Müll. Arg.
6. Thallus bright yellow to orange; spermatia ellipsoidal, straight ..... *Icmadophila* Trev.
7. Thallus crustose, uniform ..... *Solenopsora* Mass.
7. Thallus effigurate 9
8. Thallus ecorticate; apothecia immersed ..... *Haematomma* Mass.
8. Thallus corticate; apothecia sessile ..... *Phlyctella* Krmphbr.
9. Paraphyses unbranched ..... *Phlyctidia* Müll. Arg.
9. Paraphyses branched and anastomosing ..... *Phlyctis* Fw.
10. Apothecia immersed in the thallus, small ..... *Myxodictyon* Mass.
10. Apothecia sessile, large .....

LECANORA

Lecanora Ach., Lichenogr. Univ. 77. 1810.

Type: not designated.

Thallus crustose, uniform, effigurate, rarely squamose or dwarf-fruticose, attached to the substrate by the hyphae of the hypothallus or of the medulla, without rhizinae, heteromerous; ecorticate or corticate; algae protococcoid. Apothecia immersed or sessile, circular; amphithecium well developed; parathecium usually absent or poorly developed; hypothecium hyaline or brownish; paraphyses unbranched, free; asci normally 8-spored, rarely 16–32-spored; ascospores hyaline, ellipsoidal to spherical, rarely reniform. Spermatia cylindric to acicular, straight or curved.

The above generic description is based on the concept of Zahlbruckner. Of the six sections into which he divided the genus, I would recognize four as distinct genera, leaving *Eulecanora* and *Placodium*. Our material belongs in *Eulecanora*, of which the key to tropical African species follows.

1. Asci 16-spored; ascospores 8–11 × 6–8 μ, disc pale flesh color; apothecia about 0.7 mm.; thallus yellowish ashy, granular, wrinkled, margin subarachnoid; Kenya ..... *L. pleospora* Müll. Arg.
1. Asci 8-spored 2
   2. Disc white to pale cervine; thallus white 3
   2. Disc yellow to cinnamon or yellowish fleshcolor 4
   2. Disc reddish flesh color 7
   2. Disc fuscous to reddish fuscous 10
   2. Disc black, at least when dry 19
3. Thallus pale gray, margin radiate-rimose with white plumose fibrils; apothecia small, angular from mutual pressure; ascospores 9–11.5 × 6–7.5 μ; on *Euphorbia;* Ruanda ..... *L. poliothallina* Lindau
3. Thallus white or reddish, tartareous, obsoletely radiate, margin inconspicuous; apothecia 1–2 mm.; ascospores 9–12 × 5–7 μ; saxicole; St. Helena ..... *L. Sanctae-Helenae* Müll. Arg.
3. Thallus verruculose, black-margined; apothecia 0.3–0.4 mm.; ascospores 11–13 × 5 μ; corticole; Angola ..... *L. Monodorae* Vainio
   4. Thallus white to ashy, margin indistinct, verruculose; apothecia 0.7–1 mm.; ascospores 12–16 × 6–8 μ; corticole; Kenya ..... *L. flavidocarnea* Vainio
   4. Thallus white-pruinose, margin slightly radiate-fibrillose, smooth; apothecia 0.5–0.6 mm.; ascospores 8–9 × 6–7 μ; corticole; Nyasaland ..... *L. Brassii* Dodge
   4. Thallus yellowish to greenish 5
5. Ascospores slender, 13 × 4 μ; apothecia 0.7–1.2 mm.; thallus verruculose; Mozambique ..... *L. carneosulphurea* Vainio
5. Ascospores broader, 7–14 × 5–8 μ 6
   6. Thallus margin black; disc yellow-fleshcolor to livid, apothecial margin granulose; ascospores 9–11 × 6–7 μ; saxicole; Eritrea ..... *L. polytropoides* Zahlbr.
   6. Thallus margin fibrillose, pale; apothecia 1.5–2 mm.; margin thick, disc pale yellow; ascospores 12–14 × 6–7.5 μ; corticole; Usambara ..... *L. usambarensis* Müll. Arg.
   6. Thallus margin indefinite, thallus granulose-verrucose to squamulose, disc yellow to slightly brownish, apothecia 0.7–1 mm., margin thin; ascospores 10.5–12 × 5–6 μ; terricole; Ruanda ..... *L. lateritica* Lindau
7. Disc pruinose 8
7. Disc not pruinose; thallus white to pale glaucous 9
   8. Disc grayish red; apothecia 0.75–1 mm.; ascospores 9.5–11 × 5.8–6 μ; terricole; Ruanda ..... *L. laterigena* Lindau
   8. Disc dark flesh color; apothecia 0.4–0.8 mm.; ascospores 9–14 × 5–7 μ; corticole; Angola ..... *L. leprosa* v. *carneola* (Vainio) Zahlbr.
9. Disc livid flesh color, margin granulose; ascospores 9–11 × 6–7 μ; saxicole; Eritrea ..... *L. polytropoides* Zahlbr.
9. Disc flesh-rufous, margin very thin; crenulate; ascospores 10–12 × 6–7 μ; corticole; Angola ..... *L. leprosa* v. *rufocarnea* (Vainio) Zahlbr.

9. Disc dark fuscous, margin entire; corticole; Mozambique.....*L. ecoronata* Vainio
9. Disc flesh color, margin thin, entire to slightly crenulate; apothecia 0.2–0.5 mm.; ascospores 10–14 × 6–10 μ; corticole; Kenya.....*L. corallina* Hue
9. Disc pale rufous, margin thin; apothecia 0.5–0.7 mm.; ascospores 11–13 × 6–7 μ; corticole; French Equatorial Africa.....*L. callimorpha* Hue
10. Thallus obsolete; apothecia 0.3–0.6 mm.; margin thin, entire; ascospores 10–13 × 6–7.5 μ; saxicole; Kenya .....*L. subcongruens* Müll. Arg.
10. Thallus yellowish 11
10. Thallus white to ashy 13
11. Thallus rimulose, thin; apothecia 1–1.5 mm.; medulla yellowish; ascospores 9–11 × 5–5.5 μ; saxicole; Socotra .....*L. socotrana* Müll. Arg.
11. Thallus rimose-areolate, black-margined, sulfur-tartareous, 1 mm. thick; medulla yellowish; apothecia substipitate, 0.5 mm.; ascospores 8–9 × 6 μ; saxicole; Usambara .....*L. pedata* Zahlbr.
11. Thallus granular or glebous; apothecial margin tumid, entire.....12
12. Apothecia 0.8(–1.5) mm.; ascospores 8 × 5.5–6 μ; thallus ashy to citrine drab; corticole; Belgian Congo .....*L. aequinoctialis* Stzbgr.
12. Apothecia 0.4 mm.; ascospores 8–9 × 4–5 μ; thallus ashy yellow to ashy; saxicole; Eritrea .....*L. africana* Zahlbr.
12. Apothecia 0.2–0.5 mm.; ascospores 10–12 × 4–5 μ; thallus ochroleucous; terricole; Eritrea .....*L. granulescens* Jatta
12. Apothecia 0.5–0.8 mm.; ascospores 10–13 × 6–9 μ; thallus sulfur greenish; corticole; Kenya .....*L. sabulosa* Steiner
13. Thallus margin white-byssine 14
13. Thallus margin black 15
13. Thallus margin inconspicuous (or not described).....17
14. Thallus glebulose, granular; apothecial margin flexuous; ascospore size not given; corticole; Abyssinia .....*L. subfusca* v. *glebulosa* Fw.
14. Thallus wrinkled, granulose; apothecia 0.5–0.75 mm.; margin entire or subcrenulate; ascospores 15 × 7 μ; corticole; Usambara....*L. subfusca* v. *leucoblephara* Müll. Arg.
15. Thallus granulose to glebulose, ashy to citrine drab; apothecia 0.8 mm., becoming angular in age; ascospores 8 × 5.5–6 μ; corticole; Congo.....*L. aequinoctialis* Stzbgr.
15. Thallus rimulose, white; apothecia up to 0.5 mm.; ascospores 10–15 × 6–7 μ; saxicole; Angola (may belong in *Aspicilia*).....*L. homaloplaca* Nyl.
15. Thallus rimulose-aerolate; apothecia 0.4–0.5 mm.; ascospores 8–10 × 4–5 μ; saxicole.....16
16. Thallus ashy to ashy yellowish; ascospores 8–9 × 4–5 μ; Eritrea.....*L. africana* Zahlbr.
16. Thallus white; ascospores 8–10 × 4.5–5 μ; Kenya.....*L. leucoplaca* Vainio
17. Thallus smooth or verrucose; apothecia 0.6 mm.; ascospores 10–14 × 6.5–7.5 μ; corticole; Kenya .....*L. rubiniza* Steiner
17. Thallus rimulose-aerolate; apothecia 0.4–0.6 mm.; ascospores 16–20 × 4 μ; corticole; Eritrea .....*L. triguttulata* Jatta
17. Thallus granulose 18
18. Ascospores 8–12 × 4–6 μ; apothecia 0.3–0.6 mm.; Abyssinia....*L. subfusca* v. *ferax* Müll. Arg.
18. Ascospores 8–14 × 5–7 μ; São Thomé and Ilha Principe.....*L. tropica* Zahlbr.
19. Thallus white or ashy, granulose 20
19. Thallus yellowish 21
20. Thallus margin white, fibrous; apothecia 0.5 mm.; ascospores 13–18 × 7–8 μ; corticole; Angola .....*L. fibrosa* Müll. Arg.
20. Thallus margin inconspicuous; apothecia 1.5 mm.; ascospores unknown; corticole; Usambara .....*L. subfusca* v. *melaleuca* Müll. Arg.
21. Hypothecium orange rufous; apothecia 1–1.5 mm.; ascospores 17–20 × 5–6 μ; corticole; Kenya .....*L. flavidonigrans* Müll. Arg.
21. Hypothecium black; ascospores 8–10 × 7–8 μ; saxicole; Socotra.....*L. notha* Müll. Arg.
21. Hypothecium hyaline; apothecia 0.5–1 mm.; not corticole.....22
22. Epithecium dark green; thallus yellow ochre; ascospores unknown; saxicole; Usambara .....*L. flavochracea* Müll. Arg.
22. Epithecium grayish black; thallus stramineous; ascospores 11–12 × 6.5–7 μ; on soil; Ruanda .....*L. latericola* Lindau

LECANORA **Brassii**, Dodge, sp. nov.

Type: Nyasaland, Kasungu Hill, corticole, L. J. Brass 17458a.

Thallus indeterminatus, 44 μ crassitudine, albus, pruinosus, margine inconspicue radiato-fibrilloso; ecorticatus; algae *Trebouxia*, cellulis 6 μ diametro;

medulla deest aut ad 15 μ crassitudine hyphis subverticalibus magnis cum crystallis hyalinis. Apothecia 0.5–0.6 mm. diametro, margine crasso, elevato, disco pallide flavo-carneo, dense pruinoso; amphithecium 105–120 μ crassitudine, cellulis algarum dense dispositis; parathecium deest; hypothecium 40 μ crassitudine, hyalinum, hyphis 3 μ diametro dense contextum; thecium 55–60 μ altitudine; paraphyses tenues, pachydermeae, apicibus clavatis; asci clavati, juventute apicibus incrassatis, protoplastis submamillatis, 42 $\times$ 12 μ; ascosporae octonae, imbricatim monostichae, dein subdistichae, hyalinae, uniloculares, late ellipsoideae, 8–9 $\times$ 6–7 μ.

Thallus crustose, indeterminate, margin inconspicuously radiate-fibrillose, white, pruinose, not changing color when moistened; cortex not differentiated; algae *Trebouxia,* cells 6 μ in diameter, in places completely filling the thallus, in others leaving a medulla, 15 μ thick, of coarse, closely woven, subvertical hyphae, penetrating between the cork cells, often with large hyaline crystals. Apothecia 0.5–0.6 mm. in diameter, margin thick, elevated, disc pale yellowish flesh colored, densely pruinose; amphithecium 105–120 μ thick, of densely packed algae; parathecium absent; hypothecium 40 μ thick, hyaline, of densely woven hyphae 3 μ in diameter; thecium 55–60 μ tall; paraphyses slender, relatively thick-walled, tips slightly clavate, epithecial gel hyaline with minute crystals (brownish in thick sections); asci clavate, tips thickened when young, protoplasts somewhat mamillate, 8-spored, about 42 $\times$ 12 μ; ascospores imbricately monostichous, becoming subdistichous, hyaline, unilocular, broadly ellipsoidal, 8–9 $\times$ 6–7 μ.

LECANORA AEQUINOCTIALIS Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 1888/9:218. 1890.

Type: Belgian Congo, Banana, at mouth of Congo River, corticole, P. Hesse.

Thallus epiphloeodal, verrucose to glebulose, thickness variable, up to 160 μ, citrine drab with a narrow black margin; cortex about 8 μ thick, gelified, of periclinal hyphae, often disappearing on the tops of the glebulae and revealing the sulfur-colored interior, but not truly sorediose; algae protococcoid?, somewhat yellowish green, cells subspherical, 3–5 μ in diameter, mostly arranged in vertical rows and filling the smaller warts, while forming a layer about 40 μ thick around the larger, hollow warts which contain a few short, loosely tangled, subvertical filaments of *Stigonema;* medulla not differentiated. Apothecia innate in the tops of the glebulae, becoming sessile at maturity, round with an entire margin at first, then becoming lobulate from the confluence of several apothecia with a somewhat crenulate margin, 0.8(–1.5) mm. in diameter, disc plane, warm sepia becoming convex when moist and appearing immarginate; amphithecium 55 μ thick, of the same structure as the thallus; parathecium 55 μ thick in the center below the hypothecium, thinning to 20 μ at the margin, very dark brown (black in thick sections); hypothecium not clearly differentiated from the parathecium; thecium about 55 μ tall; paraphyses conglutinate, slender, tips not thickened in the brownish epithecial gel; asci clavate, thick-walled when young, 8-spored, about 40 $\times$ 8 μ; ascospores hyaline, unilocular, relatively thick-walled, subspherical, 8 $\times$ 5.5–6 μ.

Stizenberger's description is brief, but our material agrees well with the characters recorded.

Nigeria: Ondo Province, Owena, on *Theobroma,* C. A. Thorold 132; Ipetu, on *Theobroma,* C. A. Thorold 130; Ina near Ibadan, on *Theobroma,* C. A. Thorold 129.

OCHROLECHIA

Ochrolechia Mass., Ricerch. Autonom. Lich. Crost. 30. 1852.

Lecanora sect. *Ochrolechia* Flagey, Mém. Soc. Emul. Doubs, 272. 1886.

Type: not designated, based on *Verrucaria parella* Wigg. and *Lichen pallescens* L.

Thallus crustose, uniform, attached to the substrate by hyphae of the hypothallus or of the medulla, without rhizinae, ecorticate or with a cortex of erect or irregularly woven, septate, gelified hyphae; algae protococcoid; medulla of thin-walled hyphae; soredia frequent. Apothecia immersed at first, then sessile, constricted at the base; amphithecium well developed; hypothecium hyaline; paraphyses branched and anastomosing in the thecial gel (similar to those of the Pertusariaceae); asci 2–8-spored; ascospores hyaline, ellipsoidal, unilocular, large. Spermogonia in verrucae, cavity often labyrinthiform; spermatiophores unicellular; spermatia long-cylindric, straight.

Ochrolechia **palmicola** Dodge, sp. nov.

Type: Sierra Leone, Sefadu (Gbense), on trunk of *Elaeis guineensis,* P. Adames, comm. F. C. Deighton M4750.

Thallus epiphloeodes, verrucosus aut rugosus, subrimoso-areolatus, albidus, 300 μ crassitudine, laevior continuiorque ad marginem lobatum minute plumoso-fibrillosum; cortex 25 μ crassitudine, hyphis conglutinatis periclinalibus 2–2.5 μ diametro, inferne tenuioribus intertextisque; stratum algarum 25 μ crassitudine, protococcoideum, cellulis 5–6 μ diametro; medulla 130 μ crassitudine, hyphis 2–3 μ diametro laxe intertextis, granulis minutis aut crystallis inspersis, dein stratum alterum inter strata cellularum suberosarum 80–105 μ crassitudine, structura simili; soralia elevata, 1 mm. diametro, soredia granularia, pallide sulfurea, 50–60 μ diametro. Apothecia sessilia, urceolata, margine integro, 1 mm. diametro, disco vinaceo-alutaceo, albo-pruinoso; amphithecium inferne 125 μ crassitudine, superne ad 50 μ tenuescens; cortex et stratum algarum ut in thallo, medulla hyphis hyalinis conglutinatis 4 μ diametro; hypothecium 25 μ crassitudine, hyphis tenuibus, periclinalibus super stratum algarum; thecium 200–210 μ altitudine; paraphyses tenues, dichotome ramosae et sparse anastomosantes; asci cylindrico-clavati, 175 $\times$ 65 μ, pachydermei, usque ad 8 μ crassitudine; ascosporae octonae, hyalinae, leptodermeae, protoplastis granularibus, uniloculares, 55 $\times$ 24 μ.

Thallus epiphloeodal, verrucose or wrinkled, somewhat rimose-aerolate, whitish, smoother and continuous toward the lobed, white, minutely plumose-fibrillose margin, 300 μ thick; cortex 25 μ thick, of conglutinate, periclinal hyphae 2–2.5 μ in diameter, more slender and interwoven below; algal layer 25 μ thick, proto-

coccoid, cells 5–6 μ in diameter; medulla about 130 μ thick above the uppermost layer of bark cells, of loosely woven hyphae 2–3 μ in diameter, inspersed with minute granules or crystals, below which is another layer 80–105 μ thick between the bark cells, of similar structure; soralia elevated, 1 mm. in diameter, soredia coarsely granular, pale sulfur-colored, about 50–60 μ in diameter. Apothecia sessile, urceolate, margin entire, 1 mm. in diameter, disc vinaceous buff, white-pruinose; amphithecium 125 μ thick below the hypothecium, thinning to 50 μ at the somewhat inflexed top; cortex and algal layer as in the thallus, medulla of vertical, conglutinate, hyaline hyphae about 4 μ in diameter, resting on the algal layer; thecium 200–210 μ tall; paraphyses slender, dichotomously branched and occasionally anastomosing in the thecial gel; asci cylindric-clavate, 8-spored, 175 $\times$ 65 μ, wall 8 μ thick when the ascospores are mature; ascospores thin-walled, hyaline, unilocular, protoplast granular, 55 $\times$ 24 μ.

Sierra Leone: Sefadu (Gbense), on trunk of *Elaeis guineensis*, P. Adames, comm. F. C. Deighton M4750, fertile, type, 4754a, sterile.

HAEMATOMMA

HAEMATOMMA Mass., Ricerche Autonom. Lich. Crost. 32. 1852.

Loxospora Mass., Ricerche Autonom. Lich. Crost. 137. 1852.
Ophioparma Norm., Nyt Mag. Naturvidensk. 7:230. 1853.

Type: *H. vulgare* Mass. (*Lecanora haematomma* Ach.). *Lichen ventosus* L. was also transferred here. *Loxospora* was based on *Lecanora elatina* Ach., probably on immature material as Massolongo failed to see the septa and reported the ascospores as unilocular. *Ophioparma* Norm. was based on *Lichen ventosus* L., *L. haematomma* Ehrh. and *L. puniceus* Smith.

Thallus crustose (to squamulose in *H. dactylopholis* (Nyl.) Zahlbr.), corticate, of subvertical, conglutinate, thin-walled hyphae; algae protococcoid; medulla of loosely woven hyphae. Apothecia usually sessile, rarely subimmersed; amphithecium present; parathecium present or absent; hypothecium hyaline; asci 8-spored; ascospores hyaline, fusiform to acicular, septate, 4–pluri-locular, protoplasts cylindric. Spermogonia in thalline warts, dark about the ostiole; spermatia cylindric, straight or curved.

1. Thallus imbricate-squamulose (resembling that of the Phyllopsoraceae); apothecia 0.5–1 mm.; ascospores 4-locular, 22–32 $\times$ 2 μ; São Thomé.....*H. dactylopholis* (Nyl.) Zahlbr.
1. Thallus crustose 2
2. Apothecia immersed or nearly so, more or less irregular; disc reddish to testaceous; Kenya .....*H. subarthonioideum* (Zahlbr.) Hillm.
2. Apothecia sessile 3
3. Disc densely white-pruinose, margin subcrenulate; Nyasaland.....*H. Brassii* Dodge
3. Disc not pruinose, blood-red, margin entire; apothecia often aggregated and angular from mutual pressure; Abyssinia .....*H. similis* Bagl.

HAEMATOMMA Brassii Dodge, sp. nov.

Type: Nyasaland, Kasungu Hill, 1100 m., corticole, L. J. Brass 17458a.

Thallus epiphloeodes, continuus, laevis vel minutissime verruculosus, subrimulosus, subpruinosus, albidus, 250 μ crassitudine, margine indistincto; cortex

15 μ crassitudine, hyphis subverticalibus tenuibus; stratum algarum 75 μ crassitudine, cellulis *Trebouxiae*, 6–8 μ diametro, sphaericis vel subangulosis pressione mutua; medulla 160 μ crassitudine, hyphis subverticalibus laxe intertextis, 3 μ diametro. Apothecia rotundata, basi constricta, juventute urceolata, margine elevato, crasso, integro, dein disco plano, dense albo-pruinoso, margine subcrenulato; amphithecium inferne 105 μ crassitudine, superne ad 30 μ tenuescens, cortex et stratum algarum ut in thallo, medulla deest; hypothecium conicum, substipitatum dein subpulvinare, centro 300 μ crassitudine, ad marginem thecii tenuescens, hyphis verticalibus conglutinatis, rare cum coloniis algarum ad 100 $\times$ 40 μ; thecium circa 80 μ altitudine; paraphyses tenues apicibus non incrassatis; asci stipitati, clavati, apicibus incrassatis, 72 $\times$ 16 μ; ascosporae octonae, hyalinae, aciculares, multiloculares, 40 $\times$ 4 μ.

Thallus epiphloeodal, continuous, smooth or very minutely verrucose, slightly rimulose and pruinose, 250 μ thick, white, margin indistinct; cortex 15 μ thick, of slender, subvertical hyphae; algal layer 75 μ thick, with occasional colonies in the medulla, *Trebouxia,* cells 6–8 μ in diameter, spherical or somewhat angular from mutual pressure; medulla 160 μ thick, of loosely woven subvertical hyphae 3 μ in diameter. Apothecia circular, constricted at the base, urceolate at first, margin elevated, thick, entire, disc concave, at maturity margin becoming subcrenulate and disc plane, densely white-pruinose; amphithecium 105 μ thick below, thinning to 30 μ above, of the same structure as the thallus but lacking the medulla on the sides of the thecium; hypothecium conic, substipitate, becoming somewhat pulvinate, 300 μ tall in the center, thinning to the margin of the thecium, of vertical conglutinate hyphae, occasionally with large, ellipsoid colonies of algae up to 100 $\times$ 40 μ which may push up into the base of the thecium, resembling internal cephalodia, but the algae clearly *Trebouxia;* thecium not sharply differentiated from the hypothecium, about 80 μ tall; paraphyses slender, septate, tips not thickened in the epithecial gel; asci stipitate, clavate, 8-spored, about 72 $\times$ 16 μ, tips thickened, protoplasts hemispheric above; ascospores acicular, multilocular, hyaline, 40 $\times$ 4 μ.

HAEMATOMMA DACTYLOPHOLIS Zahlbr., Cat. Lich. Univ. 5:765. 1928.

Lecanora dactylopholis Nyl., Flora 69:172. 1886.

Type: São Thomé, Bom Successo, 1050–1250 m., A. Moller.

Thallus epiphloeodal, imbricate-squamulose, squamules whitish, 0.5 mm. in diameter, white-puberulent below, often with dactyloid fibrils above, up to 1–2 mm. long, crowded. Apothecia 0.5–1 mm. in diameter, constricted at the base, disc pale testaceous or pale yellowish; amphithecium crenate; asci 8-spored; ascospores acicular, 3-septate, 22–32 $\times$ 2 μ; paraphyses not very distinct, epithecium and hypothecium hyaline.—Nylander.

Only a single small thallus, with 8 apothecia on a small twig, was available for study. The thallus was probably somewhat immature, small discrete squamules on a black hypothallus, up to 0.5 mm. in diameter, margins dactyloid, ascending

but not reaching the dimensions recorded by Nylander, about 130 μ thick; cortex 16 μ thick, of erect hyphae 2–3 μ in diameter; algal layer 35 μ thick, *Trebouxia*, cells 6–8 μ in diameter; medulla 55 μ thick, of loosely woven vertical hyphae; hypothallus 25 μ thick, of periclinal hyphae 6–8 μ in diameter, septate, somewhat brownish, with occasional short rhizinal branches. Apothecia 0.5–1 mm., constricted at the base; amphithecium crenate, 130 μ thick below the thecium, 80 μ thick on the sides where the algal cells are more crowded and the medulla is absent; no parathecium; hypothecium 55 μ thick, of slender, densely woven hyphae; thecium 60 μ tall; paraphyses slender, conglutinate, tips not thickened in the pale epithecial gel; asci subcylindric, 8-spored, about 30 $\times$ 8 μ; ascospores 4-locular, acicular, hyaline, about 22 $\times$ 2 μ.

Sierra Leone: Sugar Loaf Mountain, 645–775 m., on twig, F. C. Deighton M4441b.

PARMELIACEAE

Thallus foliose, resupinate to erect and almost fruticose, but always dorsiventral, usually attached to the substrate by rhizinae; usually corticate on both surfaces (ecorticate below in *Anzia* and *Pannoparmelia*); algae protococcoid, lower surface nearly nude or more usually covered with rhizinae, which rarely anastomose to form a spongy hypothallus (*Anzia* and *Pannoparmelia*). Apothecia circular, sessile to short-stipitate; amphithecium well developed; parathecium absent or inconspicuous; paraphyses branched or unbranched; asci 8-spored (16–32-spored in *Anzia* and *Candelaria*, 2–4-spored in *Menegazzia*); ascospores unilocular, hyaline (septate in *Megalopsora* and *Physcidia*).

Of the dozen genera, all but *Parmelia* are characteristic of subarctic and temperate zones, or are endemic on other continents.

PARMELIA

PARMELIA Ach., Meth. Lich. 153. 1803.

Imbricaria Ach., K. Vetensk. Akad. Nya Handl. 15, 250. 1794.
Physcia S. F. Gray, Nat. Arr. Brit. Pl. 1:455. 1821, *non* Schreber, 1791.

Type: *Lichen saxatilis* L.

Thallus foliose, appressed or ascending, laciniate with rounded or linear lobes, often imbricate; upper surface often sorediose or isidiose, lower surface either darker or lighter than the upper, usually covered with rhizinae except at the margins (absent in subg. *Hypogymnia*); upper cortex of vertical hyphae forming a pseudoparenchyma, lower cortex usually similar (but of periclinal hyphae in the Antarctic sect. *Physcioideae*); medulla of loosely woven, mostly periclinal hyphae; algae protococcoid. Apothecia on the upper surface, never marginal, sessile or short-stipitate, disc concave to flat, often chestnut brown; amphithecium prominent; parathecium poorly developed or absent; hypothecium with algae below; paraphyses imbedded in a gel, usually somewhat branched above the asci, septate, tips clavate or pointed; asci clavate, usually 8-spored; ascospores hyaline, unilocular. Spermogonia immersed in the surface of the thallus or amphithecium,

spherical or pyriform, opening by blackened ostioles; wall black or dark brown above, light brown to hyaline below; spermatiophores simple or branched; spermatia cylindric or fusiform, often slightly constricted in the middle.

Only the sections *Hypothrachyna* and *Amphigymnia* are represented in our collections, although the section *Xanthoparmelia* has been reported from our area.

HYPOTRACHYNA

1. Thallus both isidiose and sorediose, rimulose, pale glaucous; corticole; Socotra.....*P. tiliacea* v. *rimulosa* Müll. Arg.
1. Thallus isidiose but not sorediose 2
1. Thallus sorediose but not isidiose 6
1. Thallus neither isidiose nor sorediose 11
2. Thallus lobes broad, isidioid dissected 3
2. Thallus lobes narrow, 3–5 mm. 4
3. Thallus glaucous, center also isidiose; Usambara.....*P. cetrata* v. *subisidiosa* Müll. Arg.
3. Thallus pale yellow, center not isidiose; apothecia 6–10 mm.; ascospores 22–25 × 12–15 μ; Socotra .....*P. Schweinfurthii* Müll. Arg.
4. Surface scrobiculate and isidiose, margins microphylline; Usambara.....*P. revoluta* v. *ambigua* Stein
4. Surface not scrobiculate nor margins microphylline 5
5. Lobes discrete, ashy white; medulla K yellow then red, C pale yellow; saxicole; French Guinea and Ivory Coast .....*P. laevigatoides* des Abb.
5. Lobes concrescent, pale glaucous; medulla K—, C—; corticole; Angola.....*P. concrescens* Vainio
6. Ends of lobes reticulate-rimose with soredia along the cracks, center with scattered or confluent soredia; Usambara .....*P. tenuirima* f. *sorediata* Müll. Arg.
6. Thallus not as above 7
7. Soredia granular, covering large areas; thallus pale glaucous, under-side yellowish, center pale fuscous; apothecia 5–10 mm.; ascospores 16–18 × 10–12 μ; Kenya.....*P. Hanningtoniana* Müll. Arg.
7. Soredia in discrete or confluent soralia 8
8. Margins ciliate; medulla C— 9
8. Margins without cilia 10
9. Soralia only in central portion of thallus; medulla K—; sterile; Eritrea.....*P. asmarana* Vainio
9. Soralia on lobes, margins confluent, sorediose, lobulate and microphylline; medulla K yellow, sometimes reddening in spots; apothecia 4–6 mm.; ascospores 9–15 × 6–8.5 μ; Usambara .....*P. usambarensis* Stnr. & Zahlbr.
10. Soralia few, laciniae longer and narrower than in the species; over mosses; Kenya .....*P. vicinior* v. *bryophila* Cengia-Sambo
10. Soralia abundant in the center with a few on the margins; thallus 10(–15) cm. in diameter, pale ashy, lobes 3–5(–7) mm. wide; medulla K—, C pink; sterile; both saxicole and corticole; Ivory Coast.....*P. Mangenoti* des Abb.
11. Thallus black below 12
11. Thallus pale fuscous, white-spotted below, ashy-glaucous above; ultimate lobes 3.5 mm. wide and long; ascospores 7–13 × 5–7.5 μ; Uganda.....*P. leptasca* Stnr. & Zahlbr.
11. Thallus pale or white below 15
12. Lobes without cilia; fertile 13
12. Lobes with cilia, K very slowly and faintly yellow; medulla K yellow then orange red, C—, KC—; on roots of orchids; Uganda.....*P. orchidophila* Dodge
13. Apothecia small, 2.5–3.5 mm. in diameter.....14
13. Apothecia 2.5–6 mm.; medulla K—; ascospores 14–18 × 9–12 μ; Angola.....*P. coronata* v. *denudata* Vainio
13. Apothecia 7–12 mm.; medulla K yellow then red; ascospores 24–34 × 12–17 μ; Fernando Po .....*P. coilocarpa* Stirton
14. Medulla K yellow; Uganda .....*P. Scottii* Vainio
14. Medulla K yellow then rufous or blood-red; ascospores 7–11 × 5–7 μ; Kenya.....*P. sensibilis* Stnr. & Zahlbr.
15. Sterile and poorly described; Tanganyika 16
15. Fertile and well described 17
16. Growing over mosses on rocks.....*P. homalotera* v. *bryophila* Cengia-Sambo
16. Corticole .....*P. tiliacea* v. *hypoleuca* Müll. Arg.

17. Apothecia 6–15 mm. in diameter; lobes 2–6 mm., densely rhizinose below (as in *P. cervicornis* Tuck.); ascospores 8–9 × 3–4 μ; Uganda.....*P. ducalis* Jatta
17. Apothecia small, sessile; lobes 1–5 mm. broad; medulla C—.....18
18. Medulla K yellow; growing over mosses; Uganda.....*P. leucorhiza* Vainio
18. Medulla K yellow then red; apothecia 2–4 mm.; ascospores 9–12 × 6–7 μ; corticole; Angola .....*P. hypocraea* Vainio

PARMELIA **orchidophila** Dodge, sp. nov.

Type: Uganda, Western Province, Toro District, Nyinabitaba, in ridge forest, 2500 m., on roots of *Tridactyla bicaudata* (Lindl.) Schltr., H. A. Omastin 1184.

Thallus 3–4 cm. diametro, 95–100 μ crassitudine, olivaceo-alutaceus, crenatus, sinibus excisis, lobis rotundatis, lobulis ultimis ad 3 mm. latitudine, marginibus ciliatis, ciliis ca. 0.5 mm. longitudine, laevis, subimpressus, albo-reticulatus, subrimulosus, inferne niger, marginibus castaneis, rhizinis nigris, semel bisve dichotome ramosis, centro thalli 1 mm. longitudine, ad margines brevioribus, omnino tectus; cortex superior 12 μ crassitudine, pseudoparenchymaticus, hyphis verticalibus adglutinatis, cellulis leptodermaticis, 5 μ diametro, granulis minutis nubilatis; stratum algarum 16–20 μ crassitudine, cellulis protococcoideis 5 μ diametro; medulla 55 μ crassitudine, hyphis periclinalibus, pachydermeis, 3 μ diametro, minutis cum granulis albis vel pallide alutaceis (aurantiacis in partibus moribundis) nubilatis, dense contexta; cortex inferior niger, 12 μ crassitudine, pseudoparenchymaticus, cellulis 4 μ diametro; rhizinae 20 μ diametro. Sterilis.

Thallus 3–4 cm. in diameter, 95–100 μ thick, deep olive buff, K very slowly light yellow, lobes rounded, crenate, sinuses excised, ultimate lobules up to 3 mm. wide, margins with cilia about 0.5 mm. long, surface smooth, slightly impressed, white-reticulate, slightly rimulose, underside black with chestnut margins; rhizinae covering the whole under-surface, black, once or twice dichotomously branched, about 1 mm. long in the center of the thallus, shorter toward the margin; upper cortex about 12 μ thick, pseudoparenchymatous, hyphae vertical, cells thin-walled, 5 μ in diameter, nubilated with minute granules; algal layer 16–20 μ thick, of compactly interwoven, mostly periclinal hyphae, heavily incrusted with minute granules white to pale buff, becoming orange in moribund thalli, K yellow then orange red, C—, KC—; lower cortex black, about 12 μ thick, of very dark brown pseudoparenchyma, cells about 4 μ in diameter; rhizinae 20 μ in diameter. Sterile.

AMPHIGYMNIA

1. Thallus isidiose (for lobulate, lacerate and microphylline margins, see No. 11 below).....2
1. Thallus with sorediose margins 6
1. Thallus without isidia or soredia 9
2. Thallus white to ashy or pale olive buff; lobes rounded, 15 mm. or more broad.....3
2. Thallus yellow-green 5
3. Isidia confined to the center of the thallus, not marginal; Usambara.....*P. nitens* f. *isidiosa* Müll. Arg.
3. Isidia on upper surface, small; medulla K yellow then ferruginous; apothecia 2–4 mm.; ascospores 9–12 × 6–8 μ; Mozambique.....*P. isidiza* Nyl.
3. Isidia abundant on margins as well as upper surface.....4
4. Isidia up to 2 mm. tall, some coralloid; medulla K—, C—, KC—; thallus K, very slowly and faintly yellowing; Sierra Leone.....*P. lobulascens* v. *isidiosissima* Dodge
4. Isidia very short, 0.5 mm. tall, almost granular; medulla K—, C bright pink to blood red; thallus K promptly yellow; Ivory Coast.....*P. pseudotinctorum* des Abb.

5. Surface rugose with isidia in the depressions; Kenya.....*P. caperata* v. *isidiophora* Steiner
5. Surface not wrinkled; center densely isidiose; Tanganyika.....*P. ecaperata* Müll. Arg.
5. Surface pale yellow, isidiose and microphylline margins; apothecia 6–10 mm., disc pale fuscous; ascospores 22–25 × 12–15 μ; Socotra.....*P. Schweinfurthii* Müll. Arg.
6. Thallus margins with short cilia 7
6. Thallus margins without cilia 8
7. Thallus impressed, pale olive buff, rugulose; medulla K—, C pink, KC—; Uganda..... .....*P. subciliaris* (Vainio) Dodge
7. Thallus rugulose, glaucous; medulla K—, C—; Abyssinia.....*P. abessinica* v. *sorediosa* Müll. Arg.
8. Thallus pale glaucous; medulla K yellow, then red; ascospores 11–15 × 11–12 μ; Cormoro Archipelago .....*P. Hildenbrandtii* Krmphbr.
8. Thallus glaucous, K—; medulla C pink; Angola.....*P. olivetorum* v. *sorediosa* Vainio
8. Thallus pale ashy, medulla K—, C—; sterile; French Guinea and Ivory Coast..... .....*P. subcetrarioides* des Abb.
9. Thallus ciliate 10
9. Thallus without cilia 17
10. Margins lobulate-incised to lacerate; thallus K yellow.....11
10. Margins not lacerate nor lobulate 13
11. Medulla K yellow, C red; thallus lobes 1.5(–2) cm. wide; Cameroons.....*P. lobulascens* Steiner
11. Medulla K—, C— 12
12. Ascospores 19–30 × 12–17 μ; thallus pale lurid, unchanged when moist; peripheral lobes up to 2 cm. wide; Usambara.....*P. amaniensis* Stnr. & Zahlbr.
12. Ascospores 14–16 × 8–10 μ; thallus glaucous, surface rugulose; Abyssinia....*P. abessinica* Nyl.
12. Ascospores 8–14 × 6.5–8 μ; thallus ashy lurid, yellow green when moist; peripheral lobes 3–5 mm. wide; Kenya .....*P. neirobiensis* Stnr. & Zahlbr.
13. Thallus margin white or very pale below.....14
13. Thallus margin deep brown to black below.....15
14. Ascospores 11–15 × 11–12 μ; Usambara.....*P. Hildenbrandtii* v. *ciliata* Müll. Arg.
14. Ascospores 14–16 × 8–10 μ; Usambara.....*P. abessinica* f. *glabrior* Stnr. & Zahlbr.
14. Ascospores 20–24 × 10–13 μ; Abyssinia.....*P. Schimperi* Müll. Arg.
15. Medulla K—; ascospores 13–17 × 5.5–7 μ; Usambara.....*P. procera* Stnr. & Zahlbr.
15. Medulla K yellow 16
16. Ascospores 19–29 × 11.5–18 μ; Usambara.....*P. eurycarpa* Stnr. & Zahlbr.
16. Ascospores 13–19(–20) × 7–10 μ; Kenya.....*P. pedicellata* Steiner
16. Ascospores 16–20 × 9–11 μ; Kenya.....*P. uberrima* Hue
17. Ascospores 15–23 × 7–11 μ; Sudan.....*P. africana* Müll. Arg.
17. Ascospores 19 × 11 μ; along Zambesi River.....*P. Menyhartii* Steiner
17. Ascospores 8–15 × 7–10 μ 19
17. Ascospores 15–18 × 7–10 μ 18
18. Apothecia 2–11 mm.; ascospores 15–17 × 7–8.5 μ; along Zambesi River..... .....*P. zambesica* Müll. Arg.
18. Apothecia 4 mm.; ascospores 14–16 × 6–7 μ; Angola.....*P. olivetorum* v. *esorediata* Vainio
18. Apothecia 7–20 mm.; ascospores 15–18 × 8–10 μ; Angola.....*P. hyporysalea* Vainio
19. Apothecia perforate 20
19. Apothecia imperforate 21
20. Ascospores 11–12 × 6–7 μ; apothecia up to 3.5 cm. in diameter; Angola..... .....*P. Soyauxii* Müll. Arg.
20. Ascospores 10–15 × 7–9 μ; apothecia 10–11 mm. in diameter; Kenya..... .....*P. pedicellata* v. *subbullata* Stnr. & Zahlbr.
21. Apothecia 2–4 mm.; ascospores 11–15 × 7–9 μ; Kenya.....*P. modesta* Hue
21. Apothecia 4–7 mm.; ascospores 9–11 × 6–7 μ; Somaliland.....*P. somaliensis* Müll. Arg.
21. Apothecia 15 mm.; ascospores 10–12 μ long; Usambara.....*P. nitens* Müll. Arg.

PARMELIA LOBULASCENS Steiner var. **isidiosissima** Dodge, var. nov.

Type: Sierra Leone, Sefadu (Gbense), on trunk of *Elaeis guineensis*, P. Adames, comm. F. C. Deighton M4754.

Thallus foliosus, 10 cm. diametro, 135–150 μ crassitudine, pallide olivaceo-alutaceus, irregulariter lobatus, lobis aliis rotundatis, usque ad 15 mm. latitudine, marginibus laevibus, crispatis, sinibus irregulariter excisis, eciliatis, aliis 3–5 mm. latitudine, erectis, marginibus isidiosis aut lobulatis; isidiis granularibus aut

stipitatis, ramosis, 2 mm. altitudine, 0.5 mm. diametro; lobulis non isidiatis raris, 1 mm. longitudine, 0.5 mm. latitudine, basi subconstrictis; superficies inferna nigra, opaca, minute rugulosa, rhizinis centralibus, lobis latioribus marginibus castaneis aut pallide brunneis, laevibus, nitentibus; lobis angustioribus aut rugulosis et nigris ad marginem aut alba cum zona marginali, 1 mm. latitudine; cortex superior ca. 25 μ crassitudine, pseudoparenchymaticus, cellulis leptodermeis 6 μ diametro, ad superficiem minoribus; stratum algarum 15–25(–40) μ crassitudine, protococcoideum, cellulis 6–8 μ diametro, minutis cum granulis; medulla ca. 65 μ crassitudine, hyphis pachydermeis, 3 μ diametro, laxe intertextis, granulis inspersis; cortex inferior niger, 15–25 μ crassitudine, pseudoparenchymaticus. Sterilis.

Thallus about 10 cm. in diameter, 135–150 μ thick, pale olive buff, K faint yellow, irregularly lobed, some lobes rounded, up to 15 mm. broad, margin smooth, crisped, sinuses irregularly excised, eciliate, other lobes only 3–5 mm. broad, more erect, margins isidiose or lobulate, bearing granular to stalked and branched isidia 2 mm. tall, 0.5 mm. in diameter; non-isidiose lobules very rare, about 1 mm. long, 0.5 mm. broad, somewhat constricted at the base; under-side black, opaque, minutely rugulose, rhizinae about 1 mm. long, black, confined to the central portion, attaching the thallus to the bark; broader lobes shading through chestnut to light brown at the margin, nearly smooth and shining; the narrower lobes either rugulose and black to the margin or abruptly white in a narrow zone about 1 mm. broad; upper cortex an irregular palisade about 25 μ thick, of thin-walled pseudoparenchyma, cells about 6 μ in diameter, somewhat smaller next the surface; algal layer 15–25(–40) μ thick, protococcoid, cells 6–8 μ in diameter with abundant minute granules; medulla about 65 μ thick, of loosely woven, thick-walled hyphae about 3 μ in diameter, more periclinal and compact below, interstices nearly filled with granules, K—, C—, KC—; lower cortex black, 15–25 μ thick, pseudoparenchymatous. Sterile.

The relationship of this variety to *P. lobulascens* is somewhat doubtful, as I have found no short, marginal cilia; the upper surface is wholly smooth and the hyphae of the medulla are more loosely woven and slightly smaller than in Steiner's description.

PARMELIA PSEUDOTINCTORUM des Abb., Bull. Inst. Franç. Afrique Noire 13:973. 1951.

Type: Ivory Coast, Mt. Tonkoni (cercle de Man), 1150 m., saxicole, H. des Abbayes; Mankono (cercle de Séguela), on granite, H. des Abbayes; Séguela, on granite, H. des Abbayes.

Thallus at least 16–20 cm. broad, 135 μ thick, pale olive buff to deep olive buff where covered by isidia, K yellow, lobes rounded, 2.5 cm. broad, sinuses not excised, surface smooth to slightly undulate in the outer 1.5 cm., the rest densely isidiose, isidia 0.2 mm. tall, simple or dichotomous; under-side black, minutely verrucose and rugulose, margins shading to isabelline, very rarely almost white; rhizinae scarce, simple, tip densely branched, less than 1 mm. long; upper cortex about

16 μ thick, a palisade of thin-walled hyphae, 5–6 μ in diameter, forming a pseudoparenchyma, somewhat nubilated with grayish granules; algal layer 15–18 μ thick, cells protococcoid, 6–8 μ in diameter; medulla 75–80 μ thick, of densely woven, periclinal hyphae, thick-walled, 3 μ in diameter, nubilated with grayish granules, K—, C blood-red, KC—; lower cortex about 15 μ thick, black, pseudoparenchymatous, cells about 3 μ in diameter. Apothecia 15 mm. broad, 10 mm. tall, stalk 3 mm. in diameter, 7 mm. tall; exciple shallowly sulcate and scrobiculate, sparsely to densely isidiose, disc concave, imperforate, margin extending 0.5 mm. beyond the thecium, isidiose on the edge; amphithecium 40–175 μ thick near the margin, of the same structure as the thallus with an algal layer under the hypothecium as well as next the upper cortex; hypothecium about 25 μ thick, of slender, periclinal, gelified hyphae, appearing almost amorphous, hyaline; thecium 40 μ tall; paraphyses slender, dichotomous, coherent, tips not thickened in the pale brownish epithecial gel; asci clavate-cylindric, 30 $\times$ 13 μ, tips thickened, protoplasts mamillate when young, 8-spored; ascospores distichous, long-ellipsoid to subfusiform, unicellular, hyaline, about 12 $\times$ 4–5 μ.

Our specimens differ in several respects from the description of H. des Abbayes; the dimensions of the thallus and isidia are greater, the exciple is more scrobiculate, and the ascospores narrower. In some respects it is intermediate between this species and *Parmelia tinctorum* Despr. from the Canaries.

Sierra Leone: Sefadu (Gbense), on trunk of *Elaeis guineensis*, P. Adames, comm. F. C. Deighton M4753.

PARMELIA **subciliaris** Dodge, comb. nov.

Parmelia nilgherrensis Nyl. v. *subciliaris* Vainio, Hedwigia 37:(40). 1898.

Type: Uganda, Ruwenzori, 0° 5′ S., 2900–3200 m., G. F. Scott-Elliott 218.

Thallus foliose, about 4 cm. in diameter, pale olive buff, lobes about 1 cm. broad, margin crenulate, upper surface K yellow, smooth to slightly impressed, rugulose, minutely rimose-areolate in the older portions, cilia about 2 mm. long, simple or once dichotomous, black, margins of some lobes capitate-sorediose, soralia about 1 mm. in diameter, rarely subconfluent; under-surface rugulose, black, somewhat lighter at the margin; upper cortex 40 μ thick, a palisade of pseudoparenchyma, cells about 6 μ in diameter; algal layer 25 μ thick, cells protococcoid, 7 μ in diameter; medulla 140 μ thick, of interwoven, thick-walled, mostly periclinal hyphae 6–7 μ in diameter, K—, C pink, KC—; lower cortex about 40 μ thick, black, pseudoparenchymatous, cells 4 μ in diameter, rhizinae about 60 μ in diameter, 3–5 mm. long, relatively few and confined to the middle of the thallus, twice or thrice dichotomously branched. Sterile.

Uganda: Ruwenzori, Western Province, Toro District, ridge forest on Nyinabitaba, 2500 m., on roots of *Tridactyla bicaudata* (Lindl.) Schltr., H. A. Omastin 1184.

PARMELIA SOYAUXII Müll. Arg., Linnaea 63:32. 1880.

Type: Angola, Pungo Andongo, Soyaux.

Thallus very large (two pieces available for study, 10 × 7 cm., and 11 × 7 cm.), 130–150 μ thick, pale olive buff to olive buff, K yellow, lobes crenate and crisped, up to 2 cm. broad, suberect, surface smooth, rimulose in the older portions, white-reticulate; under-side black, minutely rugulose; rhizinae very few, simple or with branched tips forming a holdfast; upper cortex 15 μ thick, of thin-walled pseudoparenchyma about 2 cells thick, heavily incrusted with minute yellowish crystals; algal layer about 30 μ thick, continuous, cells protococcoid, 5–6 μ in diameter; medulla 80 μ thick, of loosely woven, mostly periclinal very thick-walled hyphae 3 μ in diameter, more densely woven next the lower cortex, K—, C blood-red, KC—; lower cortex 12–15 μ thick, of septate, brown, conglutinate hyphae about 6 μ in diameter, cracking away and leaving the lower closely woven hyaline hyphae of the medulla to form a new pale buff cortex. Apothecia perforate, up to 3.5 cm. in diameter, exciple smooth like the thallus, margin crenate, stalk 4 mm. in diameter, 1 cm. tall, disc deeply concave at first, becoming nearly plane in very old apothecia; amphithecium extending about 500 μ beyond the thecium, inrolled when dry, 180–200 μ thick near the margin, of the same structure as the thallus but the medullary hyphae more densely interwoven and less periclinal throughout, algal layer under the hypothecium similar to that under the cortex which is almost completely gelified with very few minute yellow crystals; hypothecium 30 μ thick, almost completely gelified but showing traces of periclinal hyphae; thecium 65 μ tall; paraphyses conglutinate; dichotomous above, tips not thickened in the very pale brownish epithecial gel; asci broadly clavate, very thick-walled at first, tips remaining thick until the spores are mature, 8-spored, 35–45 × 14–18 μ; ascospores ellipsoid, unilocular, hyaline, 11–12 × 6–7 μ. Spermogonia oblate-spheroid, up to 130 μ in diameter, 105 μ tall, immersed in the medulla, neck about 15 μ long, 25 μ in diameter, wall wholly carbonaceous at maturity, pseudoparenchymatous; spermatiophores simple or dichotomous near the base, about 20 × 1 μ; spermatia cylindric, straight, 16–18 × 1 μ.

After the thecium disintegrates, the hypothecium functions as a cortex, leaving a slightly rugulose surface concolorous with the thallus, but not white-reticulate. Müller Argau evidently had only young apothecia ("parvula"), as young apothecia only 2–4 mm. in diameter are also present in our material. In habit, our plants suggest *Parmelia latissima* Fée, but internal structure is quite different.

Sierra Leone: Picket Hill (Colony), 740 m., T. S. Jones, comm. F. C. Deighton M4592.

USNEACEAE

Thallus fruticose, erect, prostrate or pendent, attached to the substrate by a hapteron, corticate with longitudinal, conglutinate hyphae in *Alectoria*, *Oropogon* and two species of *Ramalina*, otherwise fastigiate, of compact, subvertical hyphae, only somewhat pseudoparenchymatous; algae protococcoid (*Trentepohlia* in *Usnea*

sect. *Roccellinae*); medulla compact to arachnoid, often with a chondroid axis or strands of thick-walled, conglutinate, parallel hyphae, variously disposed. Apothecia circular, sessile or stipitate; amphithecium well developed; asci 1–8-spored; ascospores hyaline or brown, unicellular to muriform, relatively thick-walled.

1. Ascospores unicellular 2
1. Ascospores bilocular; cortex fastigiate 10
1. Ascospores muriform, large; asci monosporous ..... *Oropogon* Th. Fr.
   2. Medulla with a variable number of strands of mechaincal tissue ..... *Letharia* Zahlbr.
   2. Medulla uniform, either arachnoid or compact and horny 3
3. Cortex of conglutinate, periclinal hyphae ..... *Alectoria* Ach.
3. Cortex fastigiate, of subvertical hyphae 4
   4. Medulla of loosely tangled hyphae 5
   4. Medulla of periclinal hyphae 7
5. Thallus hollow 6
5. Thallus not hollow, dorsi-ventrally flattened ..... *Evernia* Ach.
   6. Thallus more or less inflated, thin ..... *Dactylina* Nyl.
   6. Thallus podetiiform, short, thick ..... *Endocoena* Crombie
7. Medulla of loosely woven hyphae; apothecia unknown ..... *Thamnolia* Ach.
7. Medulla either horny, cartilaginous, or inner portion differentiated as a chondroid axis 8
   8. Thallus podetiiform, relatively short, often coralloid; apothecia unknown ..... *Siphula* Fr.
   8. Thallus fruticose, usually much longer 9
9. Thallus flattened, whole medulla compact, algal layer lacking below ..... *Everniopsis* Nyi.
9. Thallus cylindric or angled, medulla loose surrounding the chondroid axis ..... *Usnea* [Hill] Wigg.
   10. Specialized mechanical tissue not developed; spermogonia black ..... *Desmaziera* Mont.
   10. Specialized mechanical tissue highly developed, thallus usually flattened; spermogonia pale ..... *Ramalina* Ach.

USNEA

Usnea Hill, Gen. Nat. Hist. 2:85. 1751; Wigg., Primit. Fl. Holsat. 90. 1780.

Type: *Lichen floridus* L.

Thallus fruticose or filamentous, usually of several compound branches, dichotomous, rarely sympodially branched, or unbranched, 1 cm. –7 m. long, erect, prostrate or pendent, attached to the substrate by a hapteron; branches thick at the base, thinning uniformly or abruptly toward the apex, 0.2–7 mm. thick, terete, angled or longitudinally sulcate or foveolate, smooth, verrucose, papillate, tuberculate or spinuliferous, continuous, areolate or annulate; soredia farinose or isidioid; cortex thin and fragile, or thick and cartilaginous, of densely woven, thick-walled, conglutinate, vertical hyphae, evanescent on the primary branches in a few species; algae usually protococcoid (*Trentepohlia* in the *Roccellinae*); medulla of loosely or compactly woven longitudinal hyphae; chondroid axis single, of thick-walled conglutinate, longitudinal hyphae, usually solid, rarely lacerate on the surface (hollow with a few arachnoid hyphae in the subg. *Eumitria*). Apothecia lecanorine, cup-shaped, plane or somewhat irregular, lateral (appearing terminal when formed near the tip of a branch, bent sharply and partly fused with the apothecium, the tip then resembling a long cilium), margin thin, smooth or scrobiculate, nude or ciliate; paraphyses conglutinate, septate, somewhat branched; asci subcylindric, 8-spored; ascospores unilocular, ellipsoid, hyaline. Spermogonia rare, immersed in the cortex, wall pale or slightly darkened; spermatiophores sparingly septate; spermatia straight, one end often slightly thicker.

Of the six subgenera, only *Eumitria* and *Euusnea* occur in our area. In preparing the following key, I have followed Motyka, Lich. Gen. Usnea Stud. Monogr. 1–651. 1936–1938, giving his geographic distributions for the various species.

1. Algae *Trentepohlia*, thallus grayish green, rigid, 5–10 cm. tall....2
1. Algae protococcoid 3
2. Thallus with soredia and abundant spinules, axis with some blackened hyphae; apothecia abundant, 3–5 mm. in diameter; Tanganyika....*U. perhispidella* Steiner
2. Thallus without soredia or spinules, axis with a narrow central cavity; apothecia rare, up to 10 mm. in diameter; Tanganyika....*U. Liechtensteinii* Steiner
3. Chondroid axis hollow in the thicker branches, partly filled with a few loosely woven hyphae; apothecia usually ciliate, rarely eciliate; thallus smooth or papillate, not scrobiculate nor tuberculate; soredia isidiose; subg. EUMITRIA....4
3. Chondroid axis solid, rarely somewhat lacerate, never with a distinct cavity; subg. EUUSNEA....9
4. Thallus distinctly angular (at least papillae in rows), smooth between the papillae; medulla white, rather thick and lax; Mozambique....*U. cristata* Mot.
4. Thallus terete, not angled nor papillae in rows....5
5. Thallus almost eramulose, with a few irregular ramuli, persistently ashy green, branches perpendicular, straight or irregularly flexuous, 2 mm. in diameter, tapering gradually to the apices; sterile 6
5. Thallus typically ramulose, branches divergent, farinose 7
6. Cavity of axis narrow; thallus olive green; Angola....*U. Welwitschiana* Mot.
6. Cavity of axis broad; thallus glaucous; Tanganyika....*U. elata* Mot.
7. Thallus fertile, not sorediose; branches somewhat inflated; apothecia 0.7–1 cm. in diameter, disc pruinose; Uganda ....*U. firmula* Mot.
7. Thallus sterile, sorediose, ashy green, often pruinose....8
8. Thallus 2 mm. in diameter, ramulose throughout; Tanganyika....*U. Baileyi* (Stirton) Mot.
8. Thallus 1–1.2 mm. in diameter, ramulose below, nude above; St. Helena, Angola to Cameroons ....*U. implicita* (Stirton) Mot.
9. Thallus foveolate or scrobiculate, not terete, epapillate, flaccid, base not blackened; FOVEATAE 10
9. Thallus terete or acutely angled, usually more rigid....15
10. Thallus 15–20 cm. long, not fruticulose, very flaccid 11
10. Thallus 3–9 cm. tall, fruticulose 12
11. Thallus sorediose; Tanganyika ....*U. terrestris* Mot.
11. Thallus not sorediose, partly somewhat fuscous, not contorted; Cameroons....*U. versicolor* Mot.
12. Thallus distinctly flattened, 3 cm. tall; fertile; not sorediose; Abyssinia.... ....*U. complanata* (Müll. Arg.) Mot.
12. Thallus never flattened, sorediose 13
13. Thallus 9 cm. tall, distinctly acutely wrinkled; Abyssinia to Kenya....*U. corrugata* Mot.
13. Thallus 6–7 cm. tall, not acutely wrinkled 14
14. Branches closely ramulose; soredia in farinose tubercules; Abyssinia to the Cormoro Archipelago ....*U. pulverulenta* (Müll. Arg.) Mot.
14. Branches sparingly and irregularly ramulose; soredia isidiose on ridges; cortex of larger branches not areolate; French Guinea southward....*U. leprosa* Mot.
15. Thallus articulate with pseudocyphellae, not papillate, 25–40 cm. long; medulla very lax; ARTICULATAE 16
15. Thallus continuous, or articulate without pseudocyphellae, often fruticulose, papillate or ramulose 21
16. Thallus 25 cm. long, regularly ramulose; Tanganyika....*U. flavescens* Mot.
16. Thallus eramulose or with an occasional ramulus, 25–40 cm. long....17
17. Pseudocyphellae elevated, farinose; thallus 25 cm. long, 2 mm. in diameter; Nigeria and Cameroons ....*U. pseudocyphellata* Mot.
17. Pseudocyphellae small, not elevated 18
18. Thallus 30 cm. long, quite rigid, joints up to 7 cm. long, more or less curved; São Thomé ....*U. speciosa* Mot.
18. Thallus flaccid, joints 1–3 cm. long, straight....19
19. Thallus smooth, more than 20 cm. long, pale green; Kenya and Tanganyika....*U. vesiculata* Mot.
19. Thallus distinctly rugose, 40 cm. long....20
20. Thallus foveolate, stramineous or pale green, not changing color in the herbarium; sterile; Eritrea and Somaliland ....*U. praelonga* Stirton
20. Thallus not foveolate, becoming lurid fuscous in the herbarium; apothecia 5 mm. in diameter; Abyssinia ....*U. rugosa* Mot.

21. Thallus never ashy green, either persistently stramineous, yellow, or becoming fuscous in the herbarium; living plants with a thin papery cortex, or if thicker, very smooth.....22
21. Thallus ashy green, rarely red, or if stramineous, papillate or tuberculate, seldom becoming brown in the herbarium 39
22. Thallus long, pendent, subarticulate or moniliform; STRAMINEAE.....23
22. Thallus short, fruticulose; GLABRATAE 30
23. Thallus pale stramineous or pale yellow, not changing color in the herbarium, subarticulate with almost no ramuli; AMOENAE 24
23. Thallus stramineous, fuscescent in the herbarium, ramulose; EUSTRAMINEAE; saxicole; Abyssinia .....*U. saxatilis* Mot.
23. Thallus stramineous, soon fuscescent in the herbarium, sulcate and angled, typically with abundant ramuli; SULCATAE 26
24. Thallus 0.6 mm. in diameter, very flaccid, medulla K reddening; Uganda and Kenya .....*U. Vainioana* Zahlbr.
24. Thallus 1–2 mm. in diameter, rigid 25
25. Ramuli abundant, branches 2 mm. thick below, very slender above; Kenya..... .....*U. exasperata* (Müll. Arg.) Mot.
25. Ramuli confined to upper portion of branches in small clusters; St. Helena.....*U. pulchella* Mot.
25. Ramuli absent or very rare, not in clusters; thallus moniliform; medulla rather dense; Kenya southward .....*U. moniliformis* Mot.
26. Thallus less deeply and distinctly sulcate 27
26. Thallus very deeply longitudinally sulcate 28
27. Thallus 0.5 mm. in diameter, somewhat compressed; East Africa... .....*U. gracilis* Ach.
27. Thallus 1.5 mm. in diameter; Kenya southward.....*U. fusca* Mot.
28. Branches 2 mm. or more in diameter, acutely angled, becoming quite slender and less angled toward the tips; Uganda .....*U. decipiens* Mot.
28. Branches about 1 mm. in diameter, less acutely angled, ramuli few and irregularly arranged; apothecia 1 cm. in diameter 29
29. Thallus 13 cm. long, ramuli very few and slender, up to 10 mm. long; exciple foveolate; Uganda .....*U. flaccida* (Müll. Arg.) Mot.
29. Thallus 40 cm. long, ramuli coarse, 5 mm. long; exciple smooth; Uganda....*U. aequatoriana* Mot.
30. Thallus subarticulate, sparingly ramulose; medulla lax; sterile; PYCNOCLADAE.....31
30. Thallus subarticulate or continuous, with abundant ramuli; medulla lax; fertile; CILIIFERAE 35
30. Thallus continuous, ramuli or spinules very crowded; medulla lax; fertile or sorediose; SCÅBRIDAE 38
30. Thallus smooth, green when fresh, very dark fuscous in the herbarium; medulla thin, compact; OSSEOLUCAE; thallus 8.5 cm. tall, 3 mm. in diameter, fruticose, rigid, sorediose; Tanganyika .....*U. incrassata* (Müll. Arg.) Mot.
31. Thallus 12–15 cm. long, pendent, flaccid, irregularly branched and ramulose; soredia in punctiform soralia 32
31. Thallus 4–10 cm. tall, flaccid, more or less regularly branched.....33
32. Thallus very indistinctly papillate; Tanganyika.....*U. hispidula* (Müll. Arg.) Zahlbr.
32. Thallus with distinct wrinkles but nearly terete, distinctly ramulose; Tanganyika southward .....*U. usambarensis* Mot.
33. Medulla K red, ramuli quite stiff, not crowded; thallus 7–10 cm. tall; Kenya southward .....*U. cartilaginea* Laur.
33. Medulla K— 34
34. Thallus 10 cm. tall; soralia in distinct tubercules; Kenya and Uganda.....*U. Haumanii* Mot.
34. Thallus 4 cm. tall, soralia in indistinct, somewhat blackened tubercules; Abyssinia to Uganda and Congo .....*U. ruwenzoriana* Mot.
35. Ramuli sparse but regularly disposed; apothecia 5 mm. in diameter; São Thomé southward .....*U. ochrophora* (Stzbgr.) Mot.
35. Ramuli close to crowded 36
36. Thallus sparingly branched, branches cylindric or indistinctly inflated; apothecia 5 mm. in diameter; Uganda .....*U. simplicissima* Mot.
36. Branches distinctly inflated, repeatedly branched 37
37. Thallus 3–5 cm. tall, becoming olivaceous in the herbarium; apothecia small; Cameroons .....*U. submollis* Steiner
37. Thallus 7–15 cm. tall, grayish green becoming deep fuscous in the herbarium; apothecia 15 mm. in diameter, cilia flaccid; Uganda and Tanganyika.....*U. ruvidescens* (Jatta) Mot.
38. Thallus 9 cm. tall, fruticose, sorediose; spinules not very dense; soredia isidiose, over most of the branches; medulla K yellow then promptly deep red; Angola to Tanganyika southward .....*U. undulata* Stirton
38. Thallus 5 cm. tall, not sorediose; spinules dense; medulla K yellow then slowly and indistinctly red; apothecia 2–3 mm. in diameter; Congo to Rhodesia.....*U. perspinosa* Mot.

39. Thallus thick, medulla thick and loosely woven, irregularly branched, apices short and thick, not filiform, smooth or coarsely tuberculate; Dendriticae 40
39. Thallus slender, medulla thin, compact 48
40. Thallus without pseudocyphellae, ramuli sparse; fertile; Cladocarpae....41
40. Thallus with pseudocyphellae, abundantly ramulose, usually fertile; Albomaculatae....44
40. Thallus with pseudocyphellae, almost eramulose, articulate, rugose with farinose spots; Serpentariae 46
41. Thallus 20 cm. long, pendent, at least 1 mm. thick, usually thicker, tips rather short and thick, sparsely ramulose, papillae rather large; medulla somewhat K reddening; apothecia 8 mm. in diameter; Tanganyika ....*U. trachyna* Mot.
41. Thallus less than 15 cm. tall, usually much shorter, rigid, fertile not sorediose....42
42. Thallus 5 cm. tall, dirty pale olive green; apothecia 15 mm. in diameter, exciple papillate; West Africa ....*U. scutata* Mot.
42. Thallus 7–15 cm. tall; apothecia up to 10 mm. in diameter; thallus ashy fuscescent in the herbarium, densely ramulose and papillate 43
43. Thallus 15 cm. tall, medulla 600 μ thick, loosely woven; apothecia cupuliform, exciple smooth; ramuli inflated; Nigeria to Angola....*U. hispida* Mot.
43. Thallus 7 cm. tall, medulla 400 μ thick; apothecia plane or deformed, exciple scrobiculate; ramuli thick, not inflated; Cameroons ....*U. Ledienii* Mot.
44. Thallus pale fuscous, white spotted; cortex firm, caespitose, branches subparallel; Abyssinia ....*U. albomaculata* Mot.
44. Thallus not white spotted 45
45. Thallus both fertile and sorediose; Abyssinia....*U. abissinica* Mot.
45. Thallus fertile, not sorediose, smooth, glabrous; cortex firm; Abyssinia to Uganda.... ....*U. obtusata* Mot.
46, Thallus olive green, medulla 900 μ thick; Cameroons southward....*U. Bornemuelleri* Steiner
46. Thallus sepia to fuscous or almost black in the herbarium, branches articulate and papillate; medulla 600 μ; Abyssinia 47
47. Branches 2–3 (–5) mm. in diameter, soredia isidiose in ridges....*U. Flotowii* Zahlbr.
47. Branches 2 mm. in diameter; apothecia rare, 10 mm. in diameter, exciple smooth.... ....*U. Flotowii* subsp. *serpentaria* Mot.
48. Medulla very thin, white, never rose; thallus fruticulose, sparingly branched, 3.5–12 (–20) cm. tall, densely ramulose; Setulosae 49
48. Medulla thicker, rose-color or if white then thallus over 25 cm. long, pendent; Elongatae 55
49. Thallus grayish green, 3.5–10 cm. tall; Densirostrae 50
49. Thallus with red or red-variegated cortex, 4–12 cm. tall; Rubigineae 52
50. Thallus 5 cm. tall, very densely ramulose throughout, divergently branched; apothecia 5 mm. in diameter; Congo ....*U. torrida* Mot.
50. Thallus irregularly ramulose, partly papillate or verrucose....51
51. Thallus 3.5 cm. tall, ramuli and tips coralloid branched; sterile; Tanganyika.... ....*U. myrioclada* (Steiner) Mot.
51. Thallus 8–10 cm. tall, ramuli unbranched; apothecia 2 cm. in diameter; Tanganyika southward ....*U. picta* (Steiner) Mot.
52. Thallus 20 cm. long, pendent, flaccid, subarticulate, not densely ramulose; medulla K yellow then red; Kenya and Uganda....*U. erubescens* (Stein) Mot.
52. Thallus fruticulose, 4–12 cm. tall, rigid, densely ramulose, medulla K—....53
53. Thallus 4 cm. tall, apothecia small; Tanganyika southward....*U. subflorida* (Zahlbr.) Mot.
53. Thallus 4–12 cm. tall, sorediose 54
54. Soralia broad, eroded; thallus 12 cm. tall; Congo....*U. bicolorata* Mot.
54. Soralia small; thallus 4–6 cm. tall, densely branched, tips blackening, red color less conspicuous than in other species of the section; Kenya to Uganda.... ....*U. Meyeri* (Stein) Mot.
55. Thallus relatively thick, more or less deformed but not angular or exactly terete, pale green, frequently branched; Ceratinae 56
55. Thallus thick, angular in cross-section, infrequently branched, green; Goniodes....59
55. Thallus slender, terete, infrequently branched, grayish green; Longissimae....61
56. Medulla rose; thallus 6 cm. tall, rather densely ramulose, pale green, axis 360 μ thick, somewhat lacerate in the middle; Congo southward....*U. acanthera* Vainio
56. Medulla white; thallus over 25 cm. long, pendent, sparsely and irregularly papillate....57
57. Medulla K at least slowly reddening or fuscescent; papillae irregularly arranged, adult branches about 2 mm. in diameter, cortex areolate-scrobiculate; Congo southward .... *U. distensa* Stirton
57. Medulla K— 58

58. Thallus 60 cm. long, axis 500 μ in diameter; ramuli close, larger, dichotomous; apothecia 10–20(–30) mm. in diameter; Angola to Tanganyika.....*U. amplissima* Stirton
58. Thallus 25 cm. long, axis 250 μ in diameter with some fuscous hyphae; ramuli distant, short, tips farinose-verrucose; sterile; St. Helena.....*U. umbrata* Mot.
59. Thallus 4 mm. in diameter, very hard; Congo .....*U. gigas* Mot.
59. Thallus rarely over 2 mm. in diameter, quite soft.....60
60. Thallus 50 cm. long, almost without ramuli, folds at angles elevated; Uganda..... .....*U. chloreoides* (Vainio) Mot.
60. Thallus more than 100 cm. long, regularly ramulose, very long, quite soft; Nigeria southward .....*U. africana* Mot.
61. Cortex well developed even on the primary branches, continuous or areolate.....62
61. Cortex of larger branches evanescent or shredded, mostly ecorticate.....64
62. Branches 0.9 mm. in diameter, ramuli sparse and irregular, 1–3 cm. long; St. Helena .....*U. Lyngei* Mot.
62. Branches up to 0.8 mm. in diameter or partly thicker and fasciate-flattened.....63
63. Thallus partly fasciate-flattened, axis solid; Cameroons.....*U. livida* Mot.
63. Thallus terete or slightly angular, deformed in larger branches; axis solid or with yellow hyphae; regularly ramulose, quite rigid; Kenya.....*U. contorta* Jatta
64. Thallus pale green, 1 mm. in diameter, ramuli 1–2(–3) cm. long, rare; Congo..... .....*U. arguta* Mot.
64. Thallus pale stramineous to ashy green, wholly ecorticate, 0.4–0.6 mm. in diameter, ramuli 0.5–1.5 cm. long, abundant; Congo to Tanganyika.....*U. trichodeodes* Vainio

USNEA LEPROSA Motyka, Lich. Gen. Usnea Stud. Monogr. 106. 1936.

Type: South Africa, Lydenburg, arboricole, Willms.

Thallus 7 cm. long, subpendent, closely divergently branched, closely ramulose below, almost without ramuli above, very flaccid, soredia pale ashy green; base attenuate, expanding rapidly and repeatedly branching, 1.3 mm. in diameter, usually distinctly articulate, more or less terete but partly foveolate, smooth, farinose from confluent soredia, ramuli close, filiform, 0.5–5 mm. long, straight, the thicker again ramulose and sorediose. Apices quite long, sparingly branched, eramulose, flexuous and sorediose; cortex 100 μ thick, soft; medulla 500 μ thick, loosely woven, white, K—; axis 250 μ in diameter. Apothecia 5 mm. in diameter, exciple smooth or with spinules; cilia few, short, thick, obtuse, sorediose; disc plane or convolute, densely farinose. Soredia isidiose on minute ridges, variable in size.

The above is based on Motyka's description, as our material is only a fragment, about 3 cm. long, with 5 apothecia and part of the cortex torn away in collecting. Such characters as are observable agree with the above description.

Sierra Leone: Sugar Loaf Mt., 600 m., on rocks in forest of upper slopes, F. C. Deighton 4441.

USNEA HISPIDA Motyka, Lich. Gen. Usnea Stud. Monogr. 589. 1938.

Usnea barbata v. *florida* f. *australis* Vainio, Cat. Welwitsch Afric. Pl. 2:396. 1901.

Type: Cameroons, Huea, arboricole, Lemperch.

Thallus about 15 cm. tall, rigid, becoming dark ashy fuscous in the herbarium, the smaller branches somewhat paler, opaque, base short, rigid, closely annulate, repeatedly sympodially branched at right angles; branches straight or slightly curved, articulate, joints inflated up to 3 mm. in diameter, papillae quite dense, irregular, conic, acute, the larger joints partly paler and rarely almost epapillate; cortex 100 μ thick, hard, slightly fuscous; medulla about 600 μ thick, loosely

woven, white, K—; axis 500 μ in diameter; ramuli close, perpendicular, 2–10 mm. long, attenuate at the base, thicker in the middle, apices smooth, the larger tuberculate and bearing apothecia. Apothecia numerous, rarely beyond 10 mm. in diameter, cupuliform; exciple smooth or with some large tubercles on the larger apothecia; cilia few, usually 4–8 per apothecium, broad at the base, conic-attenuate above, smooth; disc concave to plane, chalky white-pruinose; ascospores hyaline, unilocular, 11 $\times$ 6 μ.

Sierra Leone: Sugar Loaf Mt., 650–775 m., F. C. Deighton M4440.

Cameroons: [Victoria], Mrs. G. Thomson.

Blasteniaceae

Thallus crustose, indeterminate or effigurate, attached to the substrate by hyphae of the prothallus or of the medulla, heteromerous, rarely homoeomerous; ecorticate or with a fastigiate cortex which rarely appears pseudoparenchymatous; algae protococcoid; sometimes corticate below in *Gasparrinia* and *Kuttlingeria*. Apothecia round, sessile or immersed, biatorine, lecideine or lecanorine, usually with an algal layer under the hypothecium; epithecium granular or powdery, usually containing chrysophanic acid (producing a purple or violet color with potassium hydroxide); paraphyses simple, septate, tips usually characteristically thickened; asci normally 8-spored, fewer in some species of *Bombyliospora;* ascospores hyaline, thick-walled, usually polari-2–4-locular (unilocular in *Protoblastenia* and *Fulgensia*, plurilocular with rounded protoplasts in *Bombyliospora*).

There is no agreement among lichenologists on the number of genera to be recognized in this difficult family. *Bombyliospora* is so distinct that it is generally recognized as a genus, although some might not include it in this family but leave it in the *Lecideaceae*. Some would recognize only *Caloplaca* or one of its synonyms for the other genera, while I am inclined to recognize all of the genera in the following key. Since many species have been described in one genus and transferred elsewhere, depending on the number of genera recognized by an author, I have prepared keys to all the species described from tropical Africa and sorted them into the genera which I recognize, but without making new combinations in order not to add to the synonymy. The whole family is badly in need of revision, especially the temperate species.

1. Apothecia biatorine, but algae may occur beneath the hypothecium 2
1. Apothecia lecideine; thallus crustose, indeterminate; ascospores polari-bilocular ..... *Huea* Dodge & Baker
1. Apothecia lecanorine 4
   2. Ascospores unilocular ..... *Protoblastenia* Steiner
   2. Ascospores polari-bilocular 3
   2. Ascospores 3–4-locular ..... *Xanthocarpia*
   2. Ascospores plurilocular, large, protoplasts lenticular or rounded ..... *Bombyliospora* DNtrs.
3. Thallus crustose, indeterminate, usually ecorticate ..... *Blastenia* Mass.
3. Thallus effigurate, usually corticate ..... *Kuttlingeria* Trev.

4. Ascospores unilocular, thallus effigurate.....*Fulgensia* Mass. & DNtrs.
4. Ascospores polari-bilocular 5
4. Ascospores 3(–4)-locular; thallus indeterminate .....*Triophthalmidium* Müll. Arg.
5. Thallus indeterminate, usually ecorticate .....*Pyrenodesmia* Mass.
5. Thallus effigurate, usually corticate both above and below.....*Gasparrinia* Tornab.

BOMBYLIOSPORA

BOMBYLIOSPORA DNtrs. in Mass., Ricerche Autonom. Lich. Crost. 114. 1852.

Psorothecium sect. *Bombyliospora* Stzbgr., Ber. Thätigk. St. Gall. Naturw. Ges. 160. 1862.

Lecania sect. *Platylecania* Müll. Arg., Flora 65:327. 1882.

Type: *Lecidea tuberculosa* Fée.

Thallus epiphloeodal, indeterminate; cortex decomposed, of periclinal hyphae; algae *Trebouxia* or protococcoid; medulla of periclinal hyphae, rather compact. Apothecia sessile, constricted at the base, large, margin persistent; amphithecium absent; parathecium light-colored, not carbonaceous, pseudoparenchymatous from radiating thick-walled hyphae; hypothecium hyaline or darkened, of periclinal, slender hyphae; paraphyses slender with clavate to pyriform tips; asci 1–8-spored; ascospores large, hyaline, ellipsoid to oblong, septate with rounded or lenticular protoplasts.

1. Ascospores under 46 μ long 2
1. Ascospores over 75 μ long 5
2. Ascospores 4-locular, 30–46 × 14–22 μ; asci 4-spored; apothecia rather dark-colored; São Thomé .....*B. thomensis* (Nyl.) Zahlbr.
2. Ascospores 6–8-locular 3
3. Ascospores 28–30 × 11–12 μ; asci 8-spored 4
3. Ascospores 20–30 × 9–13 μ; Tanganyika.....*B. dominguensis* v. *intermedia* (Müll. Arg.) Zahlbr.
4. Hypothecium hyaline, thecium 65 μ tall; disc dark fuscous, margin orange; thallus up to 80 μ thick; Nigeria.....*B. nigeriensis* Dodge
4. Hypothecium yellowish; thecium 90–95 μ tall; disc orange or tawny, margin paler; thallus 100 μ thick; Tanganyika .....*B. cerinella* Zahlbr.
5. Hypothecium pale 6
5. Hypothecium dark 7
6. Thallus cervine ashy, isidio-tartareous; disc very dark brown; ascospores solitary, 80 × 20 μ; Tanganyika .....*B. Meyeri* Stein
6. Thallus grayish olive, rugulose verrucose; disc orange, margin white; asci 3–4-spored; ascospores 67–70 × 12–14 μ; Nigeria.....*B. Thoroldi* Dodge
7. Thallus pale glaucous, tuberculate; hypothecium vinous above "on undulated staffs, tipped a deep-blue colour"; ascospores probably solitary, about 80–110 × 20–30 μ; Nigeria .....*B. endoleucites* (Stirton) Zahlbr.
7. Thallus pale yellowish, rugulose granulose, farinose; disc pruinose then fuscous; hypothecium rufo-fulvous to rufo-fuscous; ascospores 90 × 23 μ; asci (2–)4-spored; Tanganyika .....*B. pruinata* (Müll. Arg.) Zahlbr.
7. Thallus olive green, rugulose and coarsely granulose; disc fuscous black; hypothecium fuscous; ascospores 75–90 × 25–33 μ; asci 3–4-spored; Gold Coast (Togoland).....*B. togoensis* (Müll. Arg.) Zahlbr.

BOMBYLIOSPORA **nigeriensis** Dodge, sp. nov.

Type: Nigeria, Ondo Province, Ipetu, on *Theobroma*, C. A. Thorold 106.

Thallus epiphloeodes, rugulosus vel laevis, continuus, ad 80 μ crassitudine, obscure olivaceo-alutaceus; cortex 15 μ crassitudine, decompositus gelifactusque, hyphis periclinalibus; stratum algarum 20 μ crassitudine, cellulis *Trebouxiae*, 3–4 μ diametro; medulla ad 45 μ crassitudine, hyphis conglutinatis periclinalibus inter-

textis. Apothecia solitaria vel aggregata, rare 3–4 concrescentia, basi constricta, 0.7–1 mm. diametro, margine aurantiaco, integro, elevato dein disco aequante; disco brunneo; parathecium 120 μ crassitudine, strato extero 15 μ crassitudine minutis cum crystallis aurantiacis, aliter hyalinum, hyphis radiantibus, pachydermeis, conglutinatis, septatis, pseudoparenchyma formantibus; hypothecium hyalinum, 40 μ crassitudine, hyphis periclinalibus, 3–4 μ diametro, pachydermeis; thecium 65 μ altitudine; paraphyses tenues, pachydermeae, super ascos dichotome ramosae, apicibus clavatis cum crystallis brunneis tectis; asci ellipsoidei, 50–55 $\times$ 15 μ; ascosporae octonae, hyalinae, ellipsoideae vel subfusiformes, protoplastis lenticularibus, 8-loculares, 27–30 $\times$ 12 μ.

Thallus epiphloeodal, rugulose or smooth, continuous, up to 80 μ thick, deep olive buff; cortex about 15 μ thick, decomposed and gelified, of mostly periclinal hyphae; algal layer 20 μ thick, cells of *Trebouxia*, 3–4 μ in diameter, closely packed or more scattered; medulla up to 45 μ thick, of conglutinate, interwoven, mostly periclinal hyphae. Apothecia solitary or aggregated, rarely 3–4 concrescent, constricted at the base, 0.7–1 mm. in diameter, margin orange, entire, elevated at first, then level with the flat, amber-brown disc; parathecium 120 μ thick below and on the sides of the thecium, the outer 15 μ orange with abundant aggregates of minute crystals, the rest hyaline, of radiating, conglutinate, thick-walled, closely septate hyphae 4–8 μ in diameter, forming a pseudoparenchyma; hypothecium 40 μ thick, hyaline, of thick-walled, mostly periclinal hyphae 3–4 μ in diameter; thecium 65 μ tall; paraphyses slender, thick-walled, dichotomously branched above the asci, tips slightly clavate, obscured by masses of brownish crystals to a depth of 15 μ in the epithecial gel; asci ellipsoidal, 8-spored, 50–55 $\times$ 15 μ; ascospores hyaline, ellipsoid to subfusiform, protoplasts lenticular, 8-locular, 27–30 $\times$ 12 μ.

This species belongs in the group with *B. cerinella* Zahlbr. from which it differs in its thinner thallus, orange margin, fuscous to almost black disc, lower thecium, hyaline hypothecium, and more septate ascospores. *B. thomensis* (Nyl.) Zahlbr. from São Thomé differs in having asci about 4-spored, ascospores larger, 30–46 $\times$ 14–22 μ, only 4-locular.

Nigeria: Ondo Province, Ipetu, C. A. Thorold 106, type; Oyo Province, Iseyin, C. A. Thorold 107; Moor plantation near Ibadan, C. A. Thorold 105; all on *Theobroma.*

Bombyliospora **Thoroldi** Dodge, sp. nov.

Type: Nigeria, Oyo Province, Iseyin, on *Theobroma*, C. A. Thorold 108.

Thallus epiphloeodes, rugulosus, verrucosus, continuus, 40 μ crassitudine, griseo-olivaceus; cortex 15 μ crassitudine, hyphis tenuibus periclinalibus conglutinatis; stratum algarum 12–15 μ crassitudine, cellulis *Trebouxiae*, 3–4 μ diametro, dense dispositis; medulla 10–13 μ crassitudine, hyphis tenuibus dense contexta. Apothecia 0.5–0.8 mm. diametro, basi constricta, margine tenui, albo, disco plano, cinnamomeo-alutaceo; parathecium hyalinum, 60–85 μ crassitudine sub hypothecio,

ad 40 μ superne tenuescens, hyphis radiantibus, pachydermeis, 4 μ diametro, pseudoparenchyma formantibus, hypothecium hyalinum vel pallide flavum, 12 μ crassitudine, hyphis tenuibus periclinalibus contextum; thecium 105 μ altitudine; paraphyses pachydermeae, conglutinatae, apicibus clavatis vel pyriformibus; asci leptodermei, apicibus non incrassatis; ascosporae ternae quaternaeve, 10-loculares, cellulis intermediis longioribus, protoplastis subcylindricis, 67–70 × 12–14 μ.

Thallus epiphloeodal, rugulose, verrucose, continuous, 40 μ thick, grayish olive; cortex 15 μ thick, cells of *Trebouxia*, 3–4 μ in diameter, closely packed but sometimes interrupted by strands of medulla; medulla 10–13 μ thick, of slender, closely interwoven hyphae. Apothecia 0.5–0.8 mm. in diameter, constricted at the base, margin thin, white, disc plane, cinnamon buff, both watery white when moist; parathecium hyaline, 60–85 μ thick below the hypothecium, thinning to 40 μ thick above, of radiating, thick-walled hyphae about 4 μ in diameter, forming a pseudoparenchyma; hypothecium hyaline or pale yellowish, 12 μ thick, of slender, mostly periclinal, interwoven hyphae; thecium 105 μ tall; paraphyses thick-walled, conglutinate, tips clavate to pyriform, ending in the pale yellowish epithecial gel; asci 3–4-spored, thin-walled, tips not thickened; ascospores hyaline, 10-locular, middle cells longer, protoplasts cylindric with corners rounded, septa and wall thick, 67–70 × 12–14 μ.

BLASTENIA

Blastenia Mass., Atti I. R. Ist. Veneto II, 3:append:101. 1852; Flora 35:575. 1852.

Type: *B. sinapisperma* (Lam.) Mass. For discussion, see Dodge & Baker, Ann. Mo. Bot. Gard. 25:611. 1938.

Thallus crustose, indeterminate, powdery, granulose or rimose, attached to the substrate by the hyphae of the prothallus or of the medulla, homoeomerous or heteromerous; ecorticate or with slightly developed cortex; algae protococcoid. Apothecia round, immersed to sessile; parathecium well developed; amphithecium absent, epithecium granular or powdery, K violet or purple; hypothecium hyaline; paraphyses simple, septate, capitate; asci 4–16-spored; ascospores hyaline, ellipsoid, polari-bilocular. Spermogonia immersed, spherical; spermatiophores septate; spermatia short, cylindric, straight.

In the following key the species with black apothecia probably belong in *Huea*, but in the absence of material, I have not wished to make the transfer. *Blastenia Brebissonii* v. *microspora* evidently belongs in *Xanthocarpia*.

1. Ascospores 3-locular, 20–24 × 12–13 μ; Angola.....*B. Brebissonii* v. *microspora* (Vainio) Zahlbr.
1. Ascospores 2-locular 2
   2. Thallus vitelline, granulose; apothecia orange, 0.5–0.8 mm.; ascospores 11–14 × 7–8 μ; Ilha Principe .....*B. pertenuescens* (Nyl.) Zahlbr.
   2. Thallus pale ochre; apothecia orange, 0.3–0.6 mm.; ascospores 12–14 × 6.5–8 μ; Mauretania .....*B. mauretaniae* (Hue) Zahlbr.
   2. Thallus olive black, granulose; apothecia black when dry, 0.2–0.3 mm.; ascospores 11–14 × 5–8 μ; Abyssinia.....*B. maurula* Müll. Arg.
   2. Thallus white 3

3. Disc ferruginous-fuscous or dark rufous, blackening; saxicole....4
3. Disc flesh-yellow; apothecia 0.5 mm.; ascospores 8–11 × 4–7 μ; Ilha Principe.....
.....*B. albidopallens* (Nyl.) Zahlbr.
3. Disc orange-red; apothecia 0.5–1.2 mm.; ascospores 15–22 × 8–12 μ; Kenya.....
.....*B. laetebunda* (Hue) Zahlbr.
3. Disc orange tawny; apothecia 0.2–0.4 mm.; ascospores 14–16 × 6–8 μ; Mauretania....
.....*B. sordida* (Hue) Zahlbr.
4. Thallus granulose; apothecia 1 mm.; ascospores 14–16 × 7–8 μ; Cormoro Archipelago .....*B. cormorensis* Lindau
4. Thallus rimulose areolate 5
5. Apothecia fuscous black, plane then convex to subspherical, pedicellate; St. Helena....
.....*B. lactescens* (Leight.) Zahlbr.
5. Apothecia fuscous, plane, margin black; apothecia 0.5–0.8 mm.; ascospores 15–19 × 4–6 μ; Ilha Principe .....*B. albidofusca* (Nyl.) Zahlbr.
5. Apothecia cinnamon fuscous, plane, margin black, 0.4 mm.; ascospores 11–13 × 6–6.5 μ; Kenya .....*B. polioterodes* (Steiner) Zahlbr.

PYRENODESMIA

Pyrenodesmia Mass., Atti I. R. Ist. Veneto II, 3:119. 1853.

Callopisma DNtrs., Giorn. Bot. Ital. II, 2:198. 1847, *non* Martius, 1827 (Gentianaceae).

Caloplaca Th. Fr., Lich. Arctoi, 218. 1860, *pro parte*.

Type: For discussion, see Dodge & Baker, Ann. Mo. Bot. Gard. 25:619. 1938.

Thallus crustose, attached to the substrate by the hyphae of the prothallus or of the medulla, without rhizinae, uniform, mostly yellow and K purple; heteromerous, ecorticate or nearly so; algae protococcoid; medulla of loosely woven, thin-walled hyphae. Apothecia round, appressed or sessile, seldom immersed, lecanorine with a well-developed amphithecium containing cortex, algal layer, and medulla; epithecium granulose to powdery, usually K violet or purple; hypothecium hyaline, lying above the algal layer; paraphyses simple, septate, capitate; asci 8-spored; ascospores hyaline, ellipsoidal to fusiform, polari-bilocular. Spermogonia immersed, with a hyaline wall; spermatiophores closely septate; spermatia short, straight, cylindric. In the following key *C.* is the abbreviation for *Caloplaca*.

1. Apothecia immersed or nearly so 2
1. Apothecia emersed to sessile and constricted at the base; disc orange, or fulvous.....4
2. Thallus dark olive, subsquamulose; apothecia 0.3–0.5 mm.; ascospores 10–14 × 4–7 μ; Eritrea .....*C. asmarensis* Jatta
2. Thallus white or nearly so, chalky, areolate; disc black; ascospores 14–16 × 7–8.5 μ; Mauretania 3
3. Thallus margin ciliate, areoles all about the same size and shape.....*C. concinnata* (Hue) Zahlbr.
3. Thallus margin not ciliate, areoles very variable in size and shape....*C. inconcinna* (Hue) Zahlbr.
4. Thallus fuscescent, disc ferruginous, blackening; ascospores 11–14 × 3.5 μ; Angola .....*C. benguellensis* (Nyl.) Zahlbr.
4. Thallus white to ashy 5
4. Thallus ferruginous to orange; apothecia and ascospores small.....6
4. Thallus citrine to yellow 7
5. Thallus granulose, disc ochraceous orange; Abyssinia.....*C. Odoardi* (Bagl.) Zahlbr.
5. Thallus subsquamulose but not effigurate, disc deep orange; ascospores 12–14 × 6 μ; Mauretania .....*P. conglobata* (Hue) Dodge
6. Thallus rimose-areolate; Mozambique.....*C. zambesica* (Müll. Arg.) Zahlbr.
6. Thallus powdery; Abyssinia.....*C. exasperata* (Bagl.) Zahlbr.
7. Thallus areolate, subeffigurate at margin; saxicole; Mozambique [may belong in *Gasparrinia*] .....*C. flava* (Müll. Arg.) Zahlbr.
7. Thallus squamulose 8

8. Squamules 0.2–0.3 mm. on black hypothallus; apothecia 0.2–0.5 mm.; ascospores 12–16 × 6–8 μ; Uganda.....*C. citrinella* (Jatta) Zahlbr.
8. Squamules 0.4–0.7 mm. on pale hypothallus; apothecia 0.4–0.5 mm.; ascospores 15–16 × 6–6.5 μ; S. Sahara.....*C. asekremensis* (Hue) Zahlbr.

PYRENODESMIA **conglobata** Dodge, comb. nov.

Lecanora (Pyrenodesmia) conglobata Hue, Mém. Soc. Bot. France 30:7. 1917.
Caloplaca conglobata Zahlbr., Cat. Lich. Univ. 7:110. 1930.

Type: Mauretania, Boulanouar, on bark of *Acacia tortilis,* Chudeau.

Thallus epiphloeodal, about 1 cm. in diameter, whitish, areolate, areoles quite convex, margin indeterminate, white-arachnoid on bark, but black, about 0.1 mm. wide where growing over the margin of *Ionaspis ascidioides;* cortex 16–20 μ thick, pseudoparenchymatous, heavily nubilated with minute yellowish crystals; algal layer 30–40 μ thick, of closely packed, protococcoid cells 5–6 μ in diameter; medulla scarcely differentiated, but closely septate, much branched hyphae penetrate the cork cells and more or less disorganize them to a depth of 550 μ. Apothecia sessile, somewhat constricted at the base, urceolate when very young, becoming plane, the margin not elevated at maturity, disc burnt sienna, flat, margin flame-scarlet; amphithecium 135 μ thick below the margin of the thecium, thinning to 65 μ at the top, of the same structure as the thallus, algae in large irregular colonies, 40–55 μ in diameter, extending to the top of the thecium when young but soon compressed to a zone below the margin of the thecium when mature by the expanding, hyaline parathecium which is about 15 μ thick below, expanding to 65 μ thick above, the outer 8 μ heavily nubilated with orange granules, of conglutinate, slender, thick-walled hyphae and forming a stipe below reaching the bark, 135 μ in diameter; hypothecium 40 μ thick in the center, thinning to the margin, of closely woven, slender hyphae becoming subvertical just below the thecium; thecium about 100 μ tall; paraphyses slender, conglutinate, repeatedly dichotomous above the asci, tips moniliform, 3 μ in diameter, heavily nubilated with orange crystals to a depth of 15 μ; asci 55 × 15 μ, ellipsoid-clavate, 8-spored; ascospores 12 × 5.5 μ, protoplasts spherical, terminal, 3 μ in diameter, connected by an isthmus, hyaline.

At maturity this species might be mistaken for *Blastenia,* as the algal zone is confined to a ring around the base of the thecium, while all the tissue on the sides of the thecium is parathecial.

Nyasaland: Kasungu Hill, 1100 m., corticole, L. J. Brass 17458a, Vernay Nyasaland Expedition, 1946.

GASPARRINIA

GASPARRINIA Tornabene, Lichenogr. Sicula 27. 1849.

Amphiloma Koerb., Syst. Lich. Germ. 110. 1854.
Aglaopisma DNtrs. in Bagl., Mem. Accad. Sci. Torino II, 17:396. 1856.

Type: G. *murorum* (Hoffm.) Tornabene. (For discussion, see Dodge & Baker, Ann. Mo. Bot. Gard. 25:622. 1938.)

Thallus crustose, effigurate or lobed and subfoliose, mostly yellow, K purple, heteromerous; corticate on both surfaces, cortex pseudoparenchymatous, cells thin-walled; algae protococcoid; medulla arachnoid, of thin-walled hyphae. Apothecia round, appressed or sessile, lecanorine; amphithecium containing cortex, algae, and medulla; epithecium granulose or powdery, usually K purple or violet; hypothecium hyaline, lying above the algal layer; paraphyses simple, septate, capitate; asci 8-spored; ascospores hyaline, ellipsoidal, polari-bilocular. Spermogonia immersed with a thin hyaline wall; spermatiophores closely septate; spermatia short, straight, cylindric. In the following key *C.* is the abbreviation for *Caloplaca.*

1. Thallus vitelline to pale yellow 2
1. Thallus deep orange to red 3
   2. Thallus thin, very narrow lobed, center verruciform; ascospores 11–18 × 6–8 μ; Uganda ..... *C. murorum* v. *granuliformis* (Vain.) Zahlbr.
   2. Thallus thin, linear lobes with dichotomous tips; apothecia 1 mm.; ascospores 10–13 × 6 μ; on maritime rocks; Angola ..... *C. flavorubens* (Nyl.) Zahlbr.
   2. Thallus vitelline, lobes crisped, margins contiguous; Annobon I. ..... *C. crispicans* (Nyl.) Zahlbr.
3. Apothecia unknown; thallus margins tuberculate, miniate-fulvous 4
3. Apothecia present 5
   4. Areoles convex, small; Socotra ..... *C. granulifera* (Müll. Arg.) Zahlbr.
   4. Areoles plane, larger; Somaliland ..... *C. ochraceofulva* (Müll. Arg.) Zahlbr.
5. Apothecia innate or nearly so, small disc miniate; Abyssinia ..... *Amphiloma debanense* Bagl.
5. Apothecia emersed to sessile 6
   6. Corticole; apothecia small; Abyssinia ..... *C. Beccarii* (Bagl.) Zahlbr.
   6. Saxicole 7
7. Ascospores 7–10 × 2–3 μ; apothecia 0.3–0.5 mm., adnate; Eritrea ..... *C. delicata* Jatta
7. Ascospores 6–8 μ broad 8
8. Ascospores 8–11 × 7–8 μ; apothecia 0.7–0.9 mm.; Angola ..... *C. elegantissima* (Nyl.) Zahlbr.
8. Ascospores 12 × 7 μ; Socotra ..... *C. deplanata* (Müll. Arg.) Zahlbr.
8. Ascospores 12–14 × 6–7 μ; apothecia 0.5–1 mm.; Socotra ..... *C. Balfourii* (Müll. Arg.) Zahlbr.

BUELLIACEAE

Thallus crustose to squamulose, simple or effigurate, without rhizinae, attached to the substrate by hyphae of the hypothallus or of the medulla; cortex variable, evanescent in some species; algae protococcoid; medulla loosely woven, of thin-walled hyphae; sometimes sorediose. Apothecia round, immersed to sessile, lecideine or lecanorine; paraphyses simple or branched above; asci normally 8-spored; ascospores smoke gray becoming brown, 2–4-locular or dwarf-muriform by a longitudinal division of one or more of the middle cells, usually with a thick wall but without a halo as in *Rhizocarpon.* Spermatia short, straight.

Usually the family is divided into two genera; *Buellia* with lecideine apothecia (parathecium highly developed and carbonaceous), and *Rinodina* (parathecium only slightly developed and hyaline, amphithecium well developed). Only *Buellia* is represented in our material.

BUELLIA

BUELLIA DNtrs., Giorn. Bot. Ital. II, 1:1:195. 1846.

Type: Of the three species originally included, we may eliminate *B. canescens* (Dicks.) DNtrs., as it belongs in sect. *Diploicia* which may deserve generic rank. Of the two remaining, Clements & Shear (Gen. Fung. 323. 1931) have chosen *B. parasema* DNtrs.

Thallus crustose, simple, margin sometimes effigurate (sect. *Diploicia*), attached to the substrate by hyphae of the hypothallus or of the medulla, without rhizinae; cortex fastigiate, often evanescent, rarely pseudoparenchymatous; algae protococcoid; medulla of interwoven thin-walled hyphae; occasionally sorediose. Apothecia appressed to sessile (immersed in sect. *Melanaspicilia*), lecideine, black unless the disc is pruinose; amphithecium absent; parathecium entire or dimidiate, carbonaceous; paraphyses capitate, epithecium dark; asci usually 8-spored; ascospores brown to black, ellipsoid, bilocular (in sect. *Eubuellia*) or 4-locular to dwarf-muriform (in sect. *Diplotomma*), with thick walls but without a halo (distinction from *Rhizocarpon* sect. *Catocarpon*).

In sect. *Melanaspicilia*, the apothecia are immersed in the thallus but its well-developed carbonaceus parathecium and small bilocular ascospores clearly relate it to *Buellia* rather than to *Rinodina* where it was placed by Zahlbruckner.

1. Apothecia innate or nearly so; saxicole; MELANASPICILIA.....2
1. Apothecia sessile; EUBUELLIA 4
2. Thallus white, rimose-areolate; ascospores 12 × 6 μ; Socotra.....*B. leucina* Müll. Arg.
2. Thallus yellowish to pale clay color, rimose-aerolate.....3
3. Apothecia 0.3–0.4 mm.; ascospores 9–10 × 5.5–6.5 μ; thallus margin inconspicuous; Socotra .....*B. innata* Müll. Arg.
3 Apothecia 0.3–0.4 mm.; ascospores 10–15 × 6–7 μ; thallus black-margined; Usambara .....*B. subimmersa* Müll. Arg.
3. Ascospores 10–12 × 6–7 μ; thallus K yellow, black-margined; Angola.....
.....*B. spuria* v. *ferruginea* Vainio
4. Thallus indistinct, evanescent or not described.....5
4. Thallus subcaerulescent; ascospores 10–12 × 5–6 μ; saxicole; Mauretania.....
.....*B. Chaudeauiana* (Hue) Zahlbr.
4. Thallus rose-color; apothecia 0.8–1 mm.; ascospores 9–12 × 5–6 μ; corticole; Usambara .....*B. Tobleri* Zahlbr.
4. Thallus olive fuscous; saxicole 8
4. Thallus yellowish to clay color 9
4. Thallus white to ashy or glaucous greenish 11
5. Medulla rose-color; ascospores 14–18 × 6–9 μ; corticole; Angola....*B. disciformis* v. *rhodina* Vainio
5. Medulla white 6
6. Disc white-pruinose; thallus K—, C red; saxicole; Abyssinia.....
.....*B. Caldesiana* v. *subpruinosa* Bagl.
6. Disc not pruinose 7
7. Apothecia 0.3 mm.; ascospores 14–16 × 7.5–8.5 μ; lignicole; Socotra.....
.....*B. disciformis* v. *oblongata* (Müll. Arg.) Zahlbr.
7. Apothecia 0.7 mm.; ascospores 24–34 × 12–16 μ; ramulicole; Kenya.....
.....*B. disciformis* v. *pachyspora* Zahlbr.
8. Apothecia 0.16–0.25 mm.; ascospores 10–13 × 7–8 μ; Socotra.....
.....*B. substigmatea* f. *obfuscata* Müll. Arg.
8. Apothecia 0.4 mm.; ascospores 10 × 5–5.5 μ; Mozambique.....*B. olivacea* Müll. Arg.
9. Thallus greenish yellow, rimulose, black-margined; ascospores 18.3 × 7–9 μ; Ascension Island .....*B. pachyospora* Mass.
9. Thallus yellow ashy; disc greenish-pruinose, margin contorted; corticole; Socotra.....
.....*B. disciformis* v. *contorta* (Müll. Arg.) Zahlbr.
9. Thallus ochraceous to clay-color 10
10. Apothecia 0.25–0.3 mm.; ascospores 8–11 × 4.5–5.5 μ; saxicole; Nyamnyam Territory between Sudan and Congo.....*B. afra* Vainio
10. Apothecia 0.3–0.6 mm.; ascospores 10–10.5 × 4–4.5 μ; corticole; Mozambique.....
.....*B. subpulchella* Vainio
11. Thallus gray-green to pale greenish olive 12
11. Thallus white or ashy 14
12. Ascospores 24–27.5 × 10–11.2 μ; thallus ashy green to green, granulose, prothallus ashy black; apothecia 0.3–1 mm., disc bluish-pruinose; corticole; Usambara.....
.....*B. crassa* Riehmer
12. Ascospores smaller, 11–15 × 5–7.5 μ.....13

13. Thallus subsquamulose, greenish gray; apothecia 0.5–0.75 mm.; terricole; Ruanda.....*B. argilliseda* Zahlbr.
13. Thallus rimulose-areolate, pale grayish olive; apothecia 0.5 mm. or aggregated in compact groups up to 2 mm. in diameter; corticole; Sierra Leone.....*B. Adamesii* Dodge
13. Thallus rimulose-areolate, olive green; apothecia 0.16–0.25 mm.; Socotra.....*B. substigmatea* Müll. Arg.
14. Medulla cinnabar red; thallus of tumid, bullate areoles, chalky white; disc very convex, ashy-pruinose; saxicole; Abyssinia.....*B. toninioides* Bagl.
14. Medulla white 15
15. Lignicole; thallus poorly developed; apothecia 0.3 mm.; ascospores 14–16 × 5–8 μ; Socotra .....*B. disciformis* v. *oblongata* (Müll. Arg.) Zahlbr.
15. Corticole 16
15. Saxicole 20
16. Asci 12-spored; ascospores 15.5–17 × 5–6.5 μ, each locule often biguttulate, then appearing falsely 4-locular; thallus black-margined; apothecia 0.3–0.4 mm.; Mozambique .....*B. subdives* v. *mozambica* Vainio
16. Asci 8-spored 17
17. Ascospores 20–25 × 7–9 μ; Mozambique.....*B. americana* v. *palmensis* (Vainio) Zahlbr.
17. Ascospores much smaller 18
18. Apothecial margin ashy, disc black; ascospores 13 × 7 μ; thallus subrimulose, very thin, ashy; Kenya .....*B. cinereocincta* Müll. Arg.
18. Apothecia wholly black 19
19. Ascospores 9–12 × 4–5 μ; thallus rimose, areoles convex, white, K orange, C red; St. Helena .....*B. approximans* (Leight.) Zahlbr.
19. Ascospores 12–15 × 5–5.5 μ; thallus areolate, whitish; Sierra Leone.....*B. Deightoni* Dodge
20. Hypothallus black, areoles white, angular, scattered or partly contiguous; apothecial margin white, crenulate at first; parathecium dimidiate; ascospores 9 × 5 μ; Socotra .....*B. albinea* Müll. Arg.
20. Hypothallus black, radiating far beyond the assimilative thallus; apothecia 0.3 mm.; ascospores 7–9 × 4–5 μ; Kenya.....*B. prosperens* Müll. Arg.
20. Hypothallus inconspicuous or forming a very narrow black margin.....21
21. Ascospores 8–9 × 4–5 μ 22
21. Ascospores 8–13 × 4–6 μ; thallus areolate, white, K yellow; apothecia small; Abyssinia .....*B. italica* v. *debanensis* Bagl.
21. Ascospores 11–16 × 5–7 μ 23
21. Ascospores 14–16 × 7.5–8.5 μ; thallus rugose-areolate, white; disc greenish-pruinose; Socotra.....*B. parasema* v. *subaeruginosa* Müll. Arg.
21. Ascospores 15–17 × 7–8 μ; thallus ashy, verrucose-areolate, K yellow; Abyssinia..... .....*B. dispersa* v. *cinerascens* Bagl.
22. Apothecia 0.1–0.2 mm.; thallus white, K slightly yellowish, with a narrow black margin; Angola .....*B. stellulata* f. *subtilis* Vainio
22. Apothecia 0.2–0.3 mm.; thallus ashy; Eritrea.....*B. paupercula* Jatta
23. Apothecia 0.5 mm.; thallus white, rimulose with a narrow black margin; Ilha Principe .....*B. delaevata* (Nyl.) Zahlbr.
23. Apothecia 0.4–0.8 mm.; thallus chalky white, rimose-areolate, without a conspicuous margin; Angola .....*B. subalbula* (Nyl.) Müll. Arg.

Buellia Adamesii Dodge, sp. nov.

Type: Sierra Leone, Sefadu (Gbense), on trunk of *Elaeis guineensis*, P. Adames, comm. F. C. Deighton M4755.

Thallus epiphloeodes, rimoso-areolatus, ca. 130 μ crassitudine, pallide griseo-olivaceus; cortex non bene evolutus; stratum algarum 25 μ crassitudine, filamentis cylindricis dense dispositis *Trentepohliae?*, 4–5 μ diametro, cellulis cylindricis aut apicibus rotundatis inter hyphas verticales, 2 μ diametro; medulla ca. 105 μ crassitudine, hyphis verticalibus tenuibus, plus minusve granulis inspersis, magis periclinalibus et compactis in strato inferno 15–20 μ crassitudine. Apothecia orbicularia, sessilia, basi constricta, solitaria 0.5 mm. diametro aut aggregata in gregibus ad 2 mm. diametro, nigra; parathecium inferne 80–95 μ crassitudine ad

10 μ superne tenuescens, pseudoparenchymaticum, cellulis leptodermeis, radiantibus, 6–7 μ diametro, brunneum; hypothecium 25 μ crassitudine, brunneum; thecium 105–120 μ altitudine; paraphyses tenues, subdichotome ramosae, cellulis terminalibus subsphericis nigro-brunneis; asci subcylindrici, 55 $\times$ 14 μ; ascosporae octonae, imbricatim monostichae, biloculares, brunneae, 14–15 $\times$ 5–6 μ.

Thallus epiphloeodal, rimose-areolate, about 130 μ thick, light grayish olive; cortex not differentiated; algal layer 25 μ thick, of closely packed, vertical filaments of *Trentepohlia?* 4–5 μ in diameter, cells cylindric or with rounded ends, between vertical hyphae 2 μ in diameter; medulla about 105 μ thick, of slender, mostly vertical, loosely woven hyphae, more or less inspersed with granules, becoming compact and periclinal in the lower 15–20 μ. Apothecia round, 0.5 mm. in diameter when solitary, often aggregated into groups up to 2 mm. in diameter, black, constricted at the base; parathecium 80–95 μ thick below the hypothecium, thinning to 10 μ at the top of the thecium, of radiating, thin-walled pseudoparenchyma, cells 6–7 μ in diameter, brown, the outer 15 μ very dark brown; hypothecium about 25 μ thick, dark brown; thecium 105–120 μ tall; paraphyses slender, not dense, somewhat dichotomous, terminal cells dark brown, subspherical, 3 μ in diameter; asci 8-spored, subcylindric, 55 $\times$ 14 μ; ascospores imbricately monostichous, bilocular, deep brown, not or slightly constricted at the septum, 14–15 $\times$ 5–6 μ.

The systematic position of this species is somewhat uncertain. The algae seem to be filaments of *Trentepohlia*, unless they are protococcoid and so distorted by mutual pressure as to appear filamentous, a condition occasionally seen in some species of the Verrucariaceae. If the filaments are *Trentepohlia*, the lichen may be related to *Catinaria* Vainio, which has hyaline ascospores. The often-elongate and variously curved (sometimes lirelliform) apothecia of the crowded aggregates closely resemble those of *Enccphalographa* (with *Palmella* algae) and are formed in the same way as those of *E. cerebrinella* (Nyl.) Zahlbr. from Kerguelen. The loosely arranged paraphyses are also very unusual in *Buellia*.

The first apothecium is round and solitary, about 0.5 mm. in diameter. After the ascospores are shed, the thecium disintegrates. From several points near the margin, or more irregularly scattered over the disc, new apothecia proliferate until the parathecia touch but do not fuse, and by mutual pressure assume very irregular shapes until the aggregate, seen from above, somewhat resembles a member of the Chiodectonaceae such as *Sarcographa*. In some of the larger groups (not sectioned) there is a suggestion of a third proliferation.

There is also a possibility that the species might be referred to *Rinodina*, as I have seen an occasional algal cell in the outer portion of the tissue which I have called the parathecium, clearly apothecial in origin, not thalline. The ascospores more closely resemble those of *Buellia*.

BUELLIA **Deightoni** Dodge, sp. nov.

Type: Sierra Leone, Njala (Kori), on *Amphimas pterocarpoides*, F. C. Deighton M4334B.

Thallus epiphloeodes, albidus, subverrucosus, margine indistincto, usque ad 55–65 μ crassitudine; cortex decompositus, gelifactus, 8–16 μ crassitudine, superne granulis inspersus; stratum algarum 27–40 μ crassitudine, cellulis *Trebouxiae* 5–6 μ diametro; medulla hyphis 2 μ diametro. Apothecia 0.3–0.4 mm. diametro, nigra, margine integro, tenui, subelevato, disco convexo, nigro, nudo; parathecium dimidiatum, 16 μ crassitudine, hyphis pachydermeis nigro-brunneis; hypothecium centro 55 μ crassitudine ad marginem tenuescens, hyphis brunneis, 4 μ diametro; thecium 55–65 μ altitudine; paraphyses tenues, super ascos dichotome ramosae, apicibus capitatis, cellulis apicalibus sphaericis, obscure brunneis, cellulis penultimis pyriformibus, pallide brunneis; asci cylindrico-clavati, 30 $\times$ 12 μ; ascosporae octonae, brunneae, biloculares, anguste ellipsoideae subcylindricaeve, ad septum non constrictae, 12–15 $\times$ 5–5.5 μ.

Thallus epiphloeodal, margin indeterminate, slightly verrucose, up to 55–65 μ thick above the outermost bark cells, whitish; cortex decomposed, gelified, 8–16 μ thick, outer portion with minute granules; algal layer 27–40 μ thick, of colonies of *Trebouxia*, cells 5–6 μ in diameter, separated by strands of vertical hyphae 6–8 μ wide; medulla of hyphae about 2 μ in diameter, blackening and disorganizing the outermost bark cells, then forming a hyaline layer about 55 μ thick, of loosely interwoven strands of hyphae between fragments of disintegrating hyaline bark cells, with an occasional whole cell or small group of bark cells, some strands of hyphae penetrating between the brown bark cells to a distance of 120 μ. Apothecia 0.3–0.4 mm. in diameter, black, margin thin, entire, slightly elevated, disc nude, black, becoming very convex; parathecium dimidiate, 16 μ thick, of dark brown, thick-walled hyphae, carbonaceous in thick sections; hypothecium about 55 μ thick in the center, thinning to the margin, of dark brown hyphae 4 μ in diameter; thecium 55–65 μ tall; paraphyses slender, not crowded in the thecial gel, dichotomous above the asci, tips capitate, terminal cells spherical, dark brown, penultimate cells pyriform, pale brown; asci cylindric-clavate, 8-spored, 30 $\times$ 12 μ; ascospores brown, bilocular, narrowly ellipsoid to subcylindric, not constricted at the septum, 12–15 $\times$ 5–5.5 μ.

Dimensions are quite variable in different portions of the same thallus and apothecium. I have given maximum dimensions, the minimum being about half those given. After the thecium disintegrates, the base remains white-powdery, so that parts of the thallus appear soraliate. It is not clear whether the thallus consists of small areoles, discrete and rounded on an inconspicuous hypothallus, bearing 1–3 apothecia each, or whether the thallus was originally continuous over a large area and the intervening tissue has weathered away.

Physciaceae

Thallus foliose, deeply lobed, appressed to the substrate or with ends of lobes erect (rarely completely erect in some species of *Anaptychia*); rhizinae usually present; corticate above and below (except in some species of *Anaptychia*); algae protococcoid. Apothecia circular, sessile, lecideine, pseudolecideine or lecanorine; paraphyses simple; asci 8-spored; ascospores brown, septate, usually 2-locular, rarely 4-locular or dwarf-muriform, with thick walls. Spermatiophores septate; spermatia short, straight.

PYXINE

Pyxine Fries, Syst. Orb. Veg. 267. 1825.

Phragmopyxine Clements, Gen. Fung. 84. 1909.

Type: *Lecidea sorediata* Ach. *Phragmopyxine* was based on *P. Eschweileri* Tuck.

Thallus foliose, deeply lobed, attached to the substrate by rhizinae; upper cortex pseudoparenchymatous from conglutinate vertical hyphae; algae protococcoid; medulla thick, of mostly periclinal hyphae; lower cortex often not sharply differentiated, of periclinal hyphae; soredia common. Apothecia lecideine, at least black and more or less carbonaceous at maturity; epithecium K violet; hypothecium dark; paraphyses simple, conglutinate; asci 8-spored; ascospores brown, 2(–4)-locular, thick-walled. Spermogonia immersed, mouth dark; spermatiophores septate; spermatia lateral, short-cylindric, straight.

1. Thallus isidiose, reticulately wrinkled, K yellow, medulla K yellow fulvescent, C—; corticole; Usambara ..... *P. retirugella* f. *isidiigera* Müll. Arg.
1. Thallus sorediose 2
1. Thallus without isidia or soredia 5
   2. Medulla yellow to orange or tawny 3
   2. Medulla white 4
3. Medulla and marginal soredia light yellow; saxicole; Abyssinia ..... *P. Meissneri* v. *sorediosa* Müll. Arg.
3. Medulla and small superficial soredia orange; corticole; Kenya ..... *P. Cocoes* v. *chrysantha* Müll. Arg.
3. Medulla tawny, small soredia white to tawny; lobes 0.5(–1) mm. wide; apothecia 0.7 mm.; ascospores 14–20 × 5–7 μ, 2(–4)-locular; corticole; Angola ..... *P. chrysantha* Vainio
   4. Lobes 3–6 mm. wide, ashy-glaucescent, soralia 0.5–1.5 mm., soredia greenish white; apothecia 0.5–0.8 mm.; ascospores 16–22 × 6–8 μ; corticole; Kenya ..... *P. dimorpha* Hue
   4. Lobes 2–3.5 mm. wide, pale yellowish, soralia spherical, 2–2.5 mm. in diameter, white; apothecia 0.7–1 mm.; ascospores 15–19 × 7–8 μ; corticole; French West Tropical Africa ..... *P. Chevalieri* Hue
   4. Lobes narrower, soredia superficial, white; apothecia not described; corticole; Usambara ..... *P. Cocoes* f. *sorediigera* Müll. Arg.
5. Thallus yellow to yellowish gray 6
5. Thallus white 7
   6. Thallus sulfur color, habit of *P. Cocoes;* medulla C orange-red; sterile; corticole; Mozambique ..... *P. sulphurans* Nyl.
   6. Thallus yellowish gray, under-side black, without rhizinae; apothecia 0.3 mm.; ascospores 12–14(–20) × 6–7.5 μ; saxicole; Annobon I. ..... *P. devertens* (Nyl.) Vainio
   6. Thallus olive buff, under-side black, without rhizinae, medulla white; sterile; Sierra Leone ..... *P. Adamesii* Dodge
7. Ascospores 17–21 μ long; thallus with habit of *P. Meissneri,* medulla K—; corticole; Abyssinia ..... *P. endoleuca* (Müll. Arg.) Vainio
7. Ascospores smaller 8

8. Lobes plane, much wider than typical *P. Cocoes;* corticole; Congo....*P. Cocoes* v. *congensis* Stein
8. Lobes convex 9
9. Epithecium greenish, lobes very convex; corticole; Usambara.....*P. Cocoes* v. *convexior* Müll. Arg.
9. Epithecium fuscous, disc convex, chalky pruinose; lobes slightly convex but never plane or concave; corticole; Socotra.....*P. convexa* Müll. Arg.

Pyxine **Adamesii** Dodge, sp. nov.

Type: Sierra Leone, Sefadu (Gbense), on trunk of *Elaeis guineensis*, P. Adames, comm. F. C. Deighton M4756a.

Thallus foliosus, olivaceo-alutaceus, centro subcrustosus, laciniae subimbricatae, lobis marginalibus subflabellatis, dichotome ramosis, apicibus ad 0.5 mm. latitudine, rotundatis, subpruinosis, 100 μ crassitudine, K—, C—; soralia elevata, rotundata, ad 0.7 mm. diametro, sorediis flavido-viridibus, granularibus, K—, C—; cortex 16 μ crassitudine, pseudoparenchymaticus, hyphis verticalibus, 3 μ diametro, cellula supera granulis inspersa; stratum algarum 15 μ crassitudine, cellulis protococcoideis; medulla alba, K—, C—, ca. 50 μ crassitudine, hyphis periclinalibus, 4–5 μ diametro, dense contexta; cortex inferior 8 μ crassitudine, hyphis nigro-brunneis periclinalibus. Sterilis.

Thallus foliose, olive buff, subcrustose in the center, laciniae subimbricate, marginal lobes subflabellate, dichotomous, apices 0.5 mm. or less wide, rounded, slightly white-pruinose, 100 μ thick, K—, C—; soralia elevated, 0.7 mm. in diameter, soredia yellowish green, granular to subisidioid, K—, C—; upper cortex 16 μ thick, pseudoparenchymatous, of vertical hyphae 3 μ in diameter, upper cell inspersed with minute granules; algal layer 16 μ thick, cells protococcoid; medulla white, K—, C—, about 50 μ thick, of densely woven periclinal hyphae 4–5 μ in diameter; lower cortex about 8 μ thick, of very dark brown periclinal hyphae. Sterile.

The thallus had been overgrown by *Parmelia lobulascens* v. *isidiosissima* and most of the algal cells had disintegrated, leaving lacunae in what is obviously the algal layer.

PHYSCIA

Physcia Vainio, Etude Lich. Brésil 1:138. 1890.

Type: The early history and synonymy of this genus are very involved, and I will postpone their consideration to a later time.

Thallus foliose, attached to the substrate by rhizinae, prostrate or outer portions of lobes erect, laciniae narrow, branched, margins sometimes ciliate; upper cortex pseudoparenchymatous from conglutinate vertical hyphae; algae protococcoid; medulla rather loosely woven of mostly periclinal hyphae; lower cortex of conglutinate, periclinal hyphae. Apothecia lecanorine, amphithecium well developed; parathecium scarcely differentiated (unless the thick black disc under the hypothecium represents a modified parathecium in sect. *Dirinaria*), disc deep reddish brown to fuscous and black, epithecium K—; paraphyses simple, usually septate; asci 8-spored; ascospores 2(–4)-locular or dwarf-muriform, brown. Spermogonia immersed or nearly so; spermatiophores septate; spermatia lateral, long cylindric or somewhat curved in a few species.

1. Hyaline below the hypothecium; EUPHYSCIA 2
1. Dark brown to black layer below the hypothecium; DIRINARIA 8
2. Thallus at least partly pruinose, soraliate; apothecia unknown 3
2. Thallus not sorediose; apothecia present 4
3. Thallus pale ashy, white-reticulate, K yellow above, medulla K—; soralia elevated; Angola ..... *P. reticulata* Vainio
3. Thallus chalky white, fuscescent, K—, medulla K—; soralia 0.5–1 mm. in diameter; Kenya ..... *P. Poncinsii* Hue
4. Thallus margins setose, apices of laciniae yellow; Usambara ..... *P. setosa* f. *vitellina* Müll. Arg.
4. Thallus subcrustose in center, radially wrinkled, marginal lobes not ciliate; apothecial margin crenulate, disc dark fuscous; saxicole; Guinea ..... *Parmelia incisa* Fr.
4. Thallus not as above 5
5. Ascospores 25–30 × 12–14 μ; apothecia 2–3 mm., margin entire, disc dark fuscous, pruinose; thallus white, smooth or partly wrinkled, pale below; Abyssinia ..... *Physcia dilatata* Nyl.
5. Ascospores 21–24 × 8–9.5 μ; apothecia 1.5 mm., margin vertically sulcate, disc rufous then black, not pruinose; thallus white to olive buff; Kenya ..... *P. Poncinsii* Hue *sensu* Dodge
5. Ascospores not over 22 μ, mostly shorter 6
6. Ascospores 16–18 × 9–11 μ; apothecia 0.4–0.7 mm., margin slightly crenulate, disc dark fuscous; thallus olive, subcrustose in center, laciniae short, smooth; Usambara ..... *P. abbreviata* Müll. Arg.
6. Ascospores 12–15 × 7–8 μ; apothecia very small; saxicole; Socotra 7
6. Ascospores (15–)18–20(–22) μ; apothecia 1 mm., margin entire, disc dark rufous, pruinose; thallus white, not pruinose, smooth; Kenya ..... *P. afra* Hue
7. Thallus dark olive green ..... *P. obscurella* Müll. Arg.
7. Thallus olive fuscous ..... *P. obscurella* v. *fusca* Müll. Arg.
8. Thallus isidiose, K yellow, medulla white, K—; ascospores (13–)16.5 × 6–6.5 μ; Ivory Coast ..... *P. isidiophora* des Abb.
8. Thallus not isidiose 9
9. Medulla some shade of deep red; sterile, and reference here doubtful as colored medullae occur in *Euphyscia* and *Pyxine* 10
9. Medulla white 11
10. Medulla purple-red; Kenya ..... *P. picta* v. *coccinea* Müll. Arg.
10. Medulla blood-red; thallus pale gray, white-pruinose; Kenya ..... *Crocynia haematina* Stein
10. Medulla red; Congo ..... *Crocynia Leopoldi* Stein
11. Thallus yellow; sterile, and reference here doubtful 12
11. Thallus white or grayish 13
12. Laciniae convex, narrow, soralia circular, soredia isidioid; Ascension Island ..... *P. flava* Müll. Arg.
12. Laciniae broader, similar to sorediose varieties of *P. picta* but intense yellow, sparingly sorediose above; Kenya ..... *P. picta* v. *flavicans* Müll. Arg.
13. Thallus ashy 14
13. Thallus pure white 16
14. Ascospores 12–15 × 5–7 μ; thallus ashy to lead-color, fuscescent; Angola ..... *P. africana* Müll. Arg.
14. Ascospores 13–18 × 5–8 μ; thallus ashy-glaucous 15
14. Ascospores 15–23 × 7–9 μ; disc ashy-pruinose, dark disc under the hypothecium much thicker than the thecium, extending part way up the sides of the thecium; thallus similar to *P. stellaris* v. *acrita*; corticole; Socotra ..... *P. endopyxinea* Müll. Arg.
15. Thallus K yellow; Ilha Principe ..... *P. palmarum* Vainio
15. Thallus K—; Angola ..... *P. areolata* Vainio
16. Ascospores 9–12 × 5–6 μ; thallus subcrustose in center [probably *Lecanora adscensionis* Ach. is a synonym]; saxicole ..... *P. ascensionis* Müll. Arg.
16. Ascospores 15–20 × 6–8 μ; lobes 1–3 mm. wide; corticole; Kenya ..... *P. singularis* Hue
16. Ascospores 18–22 × 6–8 μ; lobes crenulate, pulverulent; saxicole; Guinea ..... *P. aegiliata* (Ach.) Nyl.
16. Ascospores 15–23 × 7–9 μ; dark disc under the thecium much thinner than the thecium; lobes with pulvinate soredia, K— yellow; saxicole; Abyssinia ..... *Hagenia picta* v. *rupicola* Bagl.

PHYSCIA PONCINSII Hue, Mém. Soc. Bot. France 28:10. 1916.

Type: Kenya, Tika River, southeast of Mt. Kenya at Blue Post, 45 km. from Nairobi on road to Fort Hall, 1500 m., Poncins.

Thallus foliose, not closely adnate, more or less circular, up to 2.5 cm. in diameter, laciniae 1–2.5 mm. wide, radiating, white to olive buff, margins and surface of lobes soraliate, soralia up to 1 mm. in diameter, convex, and coarsely granular; upper cortex 20–40 μ thick, pseudoparenchymatous from vertical thin-walled hyphae, cells mostly 6–8 μ in diameter, upper portion heavily nubilated with grayish granules; algal layer 20–40 μ thick, of protococcoid cells 5–8 μ in diameter, continuous and closely packed; medulla 100–200 μ thick, of loosely woven, periclinal hyphae 3–4 μ in diameter, heavily nubilated with minute brownish granules; lower cortex 20–40 μ thick, of conglutinate thick-walled hyaline hyphae, the outer 6–8 μ nubilated with dark brown granules; rhizinae 60–75 μ in diameter, long, white, finally darkening. Apothecia elevated, cupulate, constricted at the base to substipitate, about 1.5 mm. in diameter, margin smooth, then vertically sulcate, inrolled, becoming completely isidio-sorediose, disc rufous at first, becoming black, not pruinose; amphithecium of young apothecia 185 μ thick, of the same structure as the thallus but the algal layer 100 μ thick on the sides of the thecium, only 60 μ thick below with cortex thickened to 60 μ; parathecium not clearly differentiated; hypothecium 15 μ thick, of dense subvertical hyphae; thecium 105 μ tall; paraphyses conglutinate, dichotomous above, tips capitate, terminal cell brownish, subspherical, 3–4 μ in diameter, nubilated with brown crystals; asci clavate, thick-walled when young, 8-spored, 65 $\times$ 16 μ; ascospores bilocular, constricted at the septum, brown, imbricately monostichous, 21–24 $\times$ 8–9.5 μ. Spermogonia flask-shaped, immersed in the medulla and the lower half of the algal layer, wall hyaline, scarcely differentiated, venter about 50 μ in diameter and 40 μ tall, neck 20 μ in diameter and 55 μ tall; spermatiophores erect, septate; spermatia bacilliform, straight, about 4–5 $\times$ 1 μ.

I hesitated to refer my material to this species, as the thallus is not pruinose, the medullary hyphae are heavily nubilated, and the dimensions of the mature thallus are twice those given by Hue. The thalli are very fragile and have been removed from the substrate. The structure of the thallus and of the soralia agrees with that given by Hue. The apothecia in the Cameroons material are immature, as only young asci are found and soralia are just beginning to form on the margins, while the Nigerian material is quite mature, ascospores varying from brown to almost black. The dimensions of the microscopic characters are identical.

Cameroons: near Kumba, on *Theobroma*, C. A. Thorold 137.

Nigeria: Majeriko near Ibadan, on *Theobroma*, C. A. Thorold 138.

Physcia abbreviata Müll. Arg., Bot. Jahrb. [Engler] 20:260. 1894.

Type: Usambara, corticole, Holst 1016 *p.p.*

Thallus foliose, small, closely appressed, smooth, 120 μ thick, margin very irregularly lobed, lobes rounded, 0.5–1 mm. wide, center subcrustose, deep olive; upper cortex 20–25 μ thick, hyaline, pseudoparenchymatous; algal layer 55 μ thick, of closely packed protococcoid cells 5–6 μ in diameter; medulla 25–40 μ thick, of compactly woven subvertical hyphae, with occasional algal cells nearly to the lower cortex; lower cortex 20–25 μ thick, of coarse, conglutinate hyphae, the outer ones brownish; rhizinae short, about 15 μ in diameter, once dichotomous

near the tip. Apothecia 0.4–0.7 mm. in diameter, sessile, not constricted at the base, margin entire to subcrenulate, concolorous with the thallus, disc opaque, fuscous black; amphithecium 55 μ thick, of the same structure as the thallus; hypothecium 15 μ thick, of deeply staining, subvertical hyphae; thecium 105 μ tall; paraphyses slender, walls gelified, dichotomous above the asci, the upper 3 cells spherical, brown, 3 μ in diameter; asci 50 $\times$ 12 μ, thick-walled and tip of the protoplast thickened when young, 8-spored, clavate; ascospores brown, bilocular, not constricted at the septum, protoplasts ellipsoid, connected by an isthmus when immature, 16–18 $\times$ 9–11 μ.

Only a single thallus about 5 $\times$ 10 mm., with four apothecia, was available for study, on a twig associated with *Ionaspis ascidioides*, *Pyrenodesmia conglobata*, and *Physcia afra* Hue. The apothecium sectioned is rather immature; the ascospores still very pale brown, 13–14 $\times$ 6–8 μ.

Nyasaland: Kasungu Hill, 1100 m., on living bark, L. J. Brass 17458a.

PHYSCIA AFRA Hue, Mém. Soc. Bot. France 28:11. 1916.

Type: Kenya, Tika River southeast of Mt. Kenya at Blue Post, 45 km. from Nairobi, on road to Fort Hall, 1500 m., corticole, Poncins.

Thallus white-opaque but not pruinose, K—, rounded, 15 mm. in diameter, laciniae 1–1.5 mm. wide near the center, narrowing to 0.3–0.6 mm. near the 2–3-fid tips, slightly convex, white below with white rhizinae; upper cortex 30–40 μ thick, pseudoparenchymatous, of vertical hyphae 8–10 μ in diameter; algal layer 40 μ thick, cells protococcoid, 6–10 μ in diameter; medulla 50–80 μ thick, of compactly woven, very thick-walled hyphae 4 μ in diameter; lower cortex 20 μ thick, of hyaline, periclinal hyphae; rhizinae short, 60 μ in diameter. Apothecia 1 mm. in diameter, constricted at the base, margin thick, prominent, entire, disc dark rufous to black, pruinose; amphithecial cortex 30 μ thick above, 40–90 μ thick below; parathecium hyaline, 12–15 μ thick above to 40 μ thick below the thecium, of periclinal hyphae above, intricate and forming the hypothecium below; paraphyses dichotomously or corymbosely branched above, tips capitate, dark rufous, 2–3 μ in diameter; ascospores brown, bilocular, distichous, (15–)18–20 (–22) μ.

I have had a single thallus with only one apothecium which was not sectioned. The macroscopic and the microscopic characters of the thallus agree with the above description which was translated from the original.

Nyasaland: Kasungu Hill, 1100 m., on living bark, L. J. Brass 17458a, Vernay Nyasaland Expedition.

ANAPTYCHIA

ANAPTYCHIA Koerb. in Mass., Mem. Lichenogr. 33. 1853.

Borrera Ach. Lichenogr. Univ. 93, 496. 1810, *p.p. min.*
Heterodermia Trev., Atti Soc. Ital. Sci. Nat. Milano 11:613. 1868.
Pseudophyscia Müll. Arg., Bull. Herb. Boissier 2:append. 1:10. 1894.

Type: not designated; *A. ciliaris* and *A. leucomelaena* treated, either of which

would conserve the genus in its present usage. *Borrera* was based on fifteen species, three now included in *Anaptychia*, the rest now in the Usneaceae, Parmeliaceae and Teloschistaceae, and the name has been abandoned. *Heterodermia* Trev. was based on seven species, all now included in *Anaptychia*. *Pseudophyscia* Müll. Arg. was based on *Lichen speciosus* Wulf.

Thallus foliose to fruticose, but always dorsi-ventral, prostrate to more or less erect, laciniae relatively narrow, branched, margins often ciliate; upper cortex of conglutinate periclinal hyphae; algae protococcoid; medulla rather loosely woven of mostly periclinal hyphae; lower cortex of conglutinate periclinal hyphae, often absent except at the margins of the lobes. Apothecia lecanorine, covered by the amphithecium until nearly mature, margin usually lacerate or lobulate; amphithecium well developed; parathecium scarcely differentiated, disc fuscous, often pruinose, epithecium K—; paraphyses simple, usually septate; asci 8-spored; ascospores bilocular, brown. Spermogonia immersed or nearly so; spermatiophores septate; spermatia lateral, short-cylindric, straight.

Most species have unusually wide geographic ranges and no species have been described based on tropical African material.

Anaptychia **Adamesii** Dodge, sp. nov.

Type: Sierra Leone, Sefadu (Gbense), on trunk of *Elaeis guineensis*, P. Adames, comm. F. C. Deighton M4752, growing over moribund *Parmelia (Amphigymnia) lobulascens* Stnr. v. *isidiosissima* Dodge.

Thallus foliosus, dichotome vel subtrichotome ramosus, laciniae ca. 1 mm. latitudine, soraliis capitatis terminalibus, 150 μ crassitudine, olivaceo-alutaceus, inferne ecorticatus, superficie arachnoidea, flava; rhizinae nigrae, nitentes, 2 mm. longitudine, dense squarroso-ramosae, marginales; cortex superior 55–65 μ crassitudine, gelifactus, hyphis periclinalibus dense contextus, strato extero 15 μ crassitudine, crystallis minutis, flavo-brunneis nubilato; stratum algarum 15–25 μ crassitudine, cellulis *Trebouxiae*, plus minusve angulosis pressione mutua, 6–7 μ diametro; medulla 60–80 μ crassitudine, hyphis pachydermeis, granulis griseis nubilatis, laxius intertextis et brunneis in strato infero, 15 μ crassitudine. Apothecia immatura, stipitata, cupularia, margine inflexo dentato; cortex amphithecialis inferne 250 μ crassitudine ad 35 μ in margine inflexo tenuescens, gelifactus, hyphis superficie perpendicularibus, in dimidia parte extera granulis brunneis nubilatis, intus griseis; stratum algarum 105 μ crassitudine circa thecium, ad 80 μ in margine tenuescens; medulla 40 μ crassitudine circum thecium; superficies thalli sub apothecio corticatus, cortex 135 μ crassitudine, structurae corticis amphithecialis similis; hypothecium 80 μ crassitudine, hyphis tenuibus subbrunneis, dense contextum; thecium ca. 110 μ altitudine; paraphyses tenues, dichotome ramosae, apicibus clavatis, 3 μ diametro; asci immaturi clavati, pachydermei, 95 $\times$ 20 μ; ascosporae non visae.

Thallus foliose, dichotomously and subtrichotomously branched, laciniae about 1 mm. broad, mostly terminating in large capitate soralia 150 μ thick, olive buff, ecorticate below, surface arachnoid, yellow becoming tawny in the older portions; rhizinae black, shining, about 2 mm. long, densely squarrose-branched, marginal,

close set, giving the appearance of laciniae on a black hypothallus; upper cortex 55–65 μ thick, highly gelified, of interwoven, mostly periclinal hyphae, the outer 15 μ nubilated with minute yellowish brown crystals; algal layer 15–25 μ thick, more or less continuous, of closely packed colonies of *Trebouxia*, cells more or less angular from mutual pressure, 6–7 μ in diameter; medulla 60–80 μ thick, of interwoven, very thick-walled hyphae about 5 μ in diameter, nubilated with grayish granules, brownish in the lower 15 μ, more loosely woven below. Apothecia immature, cupulate, stipitate, margin inflexed, dentate; amphithecial cortex 250 μ thick below, thinning to 35 μ thick over the thecium, highly gelified, hyphae perpendicular to the surface, forming a pseudoparenchyma, heavily nubilated with granules, brownish in the outer half, grayish within; algal layer 105 μ thick around the thecium, thinning to 80 μ thick above it, outer surface of the layer dentate; medulla about 40 μ thick around the thecium, not extending above it; under-side of the thallus corticate below the thecium, cortex 135 μ thick, similar in structure to that of the amphithecium; hypothecium about 80 μ thick, of densely woven, slender, slightly brownish hyphae; thecium about 110 μ tall; paraphyses slender, dichotomous, tips capitate-clavate, 3 μ in diameter; immature asci clavate, about 95 $\times$ 20 μ, thick-walled; ascospores not seen.

Fungi

Mytilidium sp.—A few hysterothecia, shaped like a clam-shell, were found on twigs of *Bauhinia tomentosa* from Njala (Kori), Sierra Leone, F. C. Deighton 4307, which do not seem referable to a previously described species, but the material is so scanty that I hesitate to describe it as new. The ascospores are brown, fusiform, 4-locular, slightly curved, about 32 $\times$ 10 μ, uniseriate in the ascus. The hysterothecia are erumpent through a lichen thallus covering the bark, but I have found no connection between the fungus and the lichen thallus. Were such a connection evident it might be referred to *Sclerographis*, from which it differs greatly in habit. The paraphyses are slender, somewhat dichotomous above the asci, but not branched and anastomosing to form an epithecium as in the Opegraphaceae, to which *Sclerographis* belongs.

GENERAL INDEX TO VOLUME XL

New scientific names of plants and the final members of new combinations are printed in **bold-face** type; synonyms and page numbers having reference to figures and plates, in *italics;* and all other matter in ordinary type.

A

Acanthographis, 311
Acanthotheciopsis, 312
Acasporaceae, 274
Actinoglyphis, 335; *Leprieurii*, 335
Africa, tropical, Some lichens of, 271
Aglaopisma, 389
Agriculture, milpa system of, in Yucatan, 51
Alectoria, 378, 379
Allarthonia, 303
Allarthothelium, 303
Almanac, Bluegrass pasture, 1
Alyxoria, 308
Amphiloma, 389; **debanense**, 390
Amphiloma, 389
Anaptychia, 399; **Adamesii**, 400; ciliaris, 399; leucomelaena, 399
Anderson, Edgar: The analysis of suspected hybrids as illustrated by Berberis × gladwynensis, 73; and William L. Brown: The popcorns of Turkey, 33
Andrews, Henry N., and Sergius H. Mamay: Some American Medullosas, 183
Animals: dispersal of Persimmon by, 217; observed at Wildwood, 245; relation between bluegrass pastures and, 1, *24*, *26*, *28*
Anomorpha, 312; *turbulenta*, 312
Anthracothecium, 273, 285; cinerosum, 285, 286; Doleschalii, 283; sect. Euanthracothecium, 285; euthelium, 285; guineense, 285, 286; lugescens, 285; sect. Porinastrum, 285; punctuliforme, 285; vitellinum, 285
Antrocarpum, 341
Anzia, 372
Archaeological: and ethnological races of maize, 79, 84; studies of the Maya civilization, 51
Arizona and New Mexico, A contribution to the lichen flora of, 63
Arthonia, 301, 303; applanata, 304; calospora, 305; carneoalbens, 304; cinnabarina, 304, v. dendritica, 304, v. elegantula, 304, v. medusaeformis, 304, v. orbicella, 304, v. reducta, 304, v. rimata, 304, v. speciosa, 304; **elevata**, 305; erythrocarpa, 304, v. roseopallens, 304; fuscescens, 308; gregaria v. dendritica, 304; ilicinodes, 304; leptogramma, 305, 306; **leptogrammodes**, 305, 306; leptographoidea, 304, 305; loangana, 304; microcarpella, 305; **modesta**, 304, 305; palmensis, 304; pertusariella, 304; somaliensis, 304; **subcaesia**, 304, 307
Arthoniaceae, 301, 303, 338
Arthoniopsis, 303
Arthopyrenia, 273, 274
Arthopyrenia sect. *Melanotheca*, 292
Arthopyreniella, 273
Arthothelium, 301, 302, 303, 326; dictyophorum, 302; laceratum, 302
Ascidium, 342; *Cinchonarum*, 342; *rhodostoma*, 343
Asiatic races of maize, cob morphology of, 87, in relation to ethnology and archaeology, 104
Asterisca, 335; *labyrinthica*, 335
Astrotheliaceae, 297
Astrothelium, 297
Aulacographa, 312
Aulaxina, 307

B

Bacidia, 352, 357; abessinica, 358; amylothelia, 358; araneosa, 358; atlantica, 358; byssothallina, 358; decussata, 358; endoleucella v. colorata, 358; sect. Eubacidia, 357, 358; exiguella, 358; farinulenta, 358; golungensis, 358, 359, v. pauciseptata, 359, 360, v. pluriseptata, 359, 360; griseoalba, 358; heteroloma, 360, v. bacteriospora, 358, 361, v. elongata, 358, 361; imitans, 358; infuscata, 358; Kotschyi, 358; leucotrypta, 358; **nigeriensis**, 358, 359; nigrocincta, 358; subg. Scoliciosporum, 274; Scottii, 358; socotrana, 358; stellaris, 358; sublecanorina, 358; submillegrana, 358; trichosperma, 358; vagula, 358; sect. Weitenwebera, 357, 358
Barberry: hybridization of, 73; relationships of two species and their putative hybrids, *74*, *76*, *77*
Bathelium, 275, 278, 280, 286, 288, 296; **compositum**, 289; duplex f. **simplicius**, 289, 290; mastoideum, 289; **papillosum**, 288, 289, 290; **porosum**, 290; **subalbens**, 289, 290
Bathelium, 296
Belonia, 273

Berberis × gladwynensis, An analysis of suspected hybrids as illustrated by, 73
Berberis, 73; × **gladwynensis**, *74*, *77*, *78*; Julianae, *74*, *77*; verruculosa, *73*, *77*
Biatora rubina, 355
Birds: list of, eating persimmon fruit, 218; found at Wildwood, 248, 256
Blastenia, 384, 387; albidofusca, 388; albidopallens, 388; Brebissonii v. microspora, 387; cormorensis, 388; lactescens, 388; laetebunda, 388; mauretaniae, 387; maurula, 387; pertenuescens, 387; polioterodes, 388; sinapisperma, 387; sordida, 388
Blasteniaceae, 384
Blastodesmia, 273
Blenothallia, 351
Bluegrass: pasture almanac, 1; pastures, *24-30*
Bombyliospora, 384, 385; cerinella, 385, 386; dominguensis v. intermedia, 385; endoleucites, 385; Meyeri, 385; **nigeriensis**, 385; pruinata, 385; thomensis, 385, 386; **Thoroldi**, 385, 386; togoensis, 385
Borrera, 399
Bottaria, 286, 290; sect. *Anthracothecium*, 285
Brass, L. J., lichens collected by, 271
Brassia, 342
Brigantiaea, 361; *argentea*, 361; *Mariae*, 361; *tricolor*, 361; *tristis*, 361
Brookhill Farm, observations on bluegrass pastures made at, 1
Brown, William L., Edgar Anderson and: The popcorns of Turkey, 73
Bryophagus, 348; *Gloeocapsa*, 348
Buellia, 355, 390; **Adamesii**, 392; afra, 391; albinea, 392; americana v. palmensis, 392; approximans, 392; argilliseda, 392; Caldesiana v. subpruinosa, 391; canescens, 390; Chaudieauiana, 391; cinereocincta, 392; crassa, 391; **Deightoni**, 392, 394; delaevata, 392; sect. Diploicia, 390; sect. Diplotomma, 391; disciformis v. contorta, 391, v. oblongata, 391, 392, v. pachyspora, 391, v. rhodina, 391; dispersa v. cinerascens, 392; sect. Eubuellia, 391; innata, 391; italica v. debanensis, 392; leucina, 391; sect. Melanaspicilia, 391; olivacea, 391; pachyspora, 391; parasema, 390, v. subaeruginosa, 392; paupercula, 392; prosperens, 392; spuria v. ferruginea, 391; stellulata f. subtilis, 392; subalbula, 392; subdives v. mozambica, 392; subimmersa, 391; subpulchella, 391; substigmatea, 392, f. obfuscata, 391; Tobleri, 391; toninioides, 392
Buelliaceae, 390
Bunodea, 280

C

Callopisma, 388
Caloplaca, 384, 388; **arizonica**, *67*, *68*; asmarensis, 388; askremensis 389; Balfouri, 390; Beccarii, 390; benguelensis, 388; cinnabarina, 69; citrinella, 389; concinnata, 388; *conglobata*, 389; crispicans, 390; delicata, 390; deplanata, 390; elegantissima, 390; exasperata, 388; flava, 388; flavorubens, 390; granulifera, 390; granuliformis, 390; inconcinna, 388; murorum, 389, 390, v. granuliformis, 390; ochraceofulva, 390; Odoardi, 388; zambesica, 388
Caloplaca, 388
Cameroons, lichens from, 271
Candelaria, 372
Candelariella, 365
Carlosia, 300
Catillaria, 352; subternella, 358
Catinaria, 338, 339, 393
Chapsa, 342; *indicum*, 343
Chicory in pastures, 13, *28*
Chiodecton, 301, 333, 337; **album**, 338; amyloplacoides, 337; amyloplacum, 337; Brunnthaleri, 338; subg. Byssophorum, 301, 337, 338; circumscissum, 337; subg. Enterographa, 337; subg. Euchiodecton, 337; hypochryseum, 338; intercedens, 338; irregulare, 337; laceratum, 337; minutulum, 337; molle, 338; mozambicum, 337; nanum, 337; palmensis, 337; rotundatum, 337; sanguineum, 337, 338; seriale, 337; socotranum, 337; sphaerale, 337
Chiodectonaceae, 333
Chiographa, 318
Chlorocyphella, 363
Chromosome knobs on Turkish popcorns, numbers and positions of, 44
Chromosomes: of Delphinium, 132, 134, 164, morphology of, 136, 147; of Diospyros, 213; of Petunia, treated with x-rays, 261
Chroodiscus, 340
Cladoxylon, 198
Clathroporina, 273, 275, 285, 296
Coal balls, fossils of Medullosa found in, 183
Cob morphology among certain archaeological and ethnological races of maize, 79
Coccotrema, 273, 287
Coenogoniaceae, 349
Coenogonium, 349; **congensis**, 350; **Deightoni**, 349; Linkii, 349

Collema, 351; aggregatum, 351; ascaridiosporum, 351; sect. Blenothallia, 351; cheila, 351; sect. Collemodiopsis, 351; conglomeratum, 351; sect. Dicollema, 351; fasciculare, 351; flaccidum, 351; haemaleia, 351; Lactuca, 351; nigrescens, 351, var. minutum, 351; rupestre, 351; *scotinum*, 351; *turgidum*, 351
Collemaceae, 351
Coniochila, 341
Contribution to the lichen flora of Arizona and New Mexico, 63
Corn, see Maize
Coscinedia, 342
Creographa, 327; *brasiliensis*, 327
Crocynia, 301, 397; haematina, 397; Leopoldi, 397
Cryptolechia, 348
Cryptothecia, 301, 302; caesioalba, 302; geniflexum, 302; nigeriensis, 302; Stirtoni, 302; subnidulans, 302; Thoroldi, 302, 303
Cryptotheciaceae, 301, 338
Cyclocarpineae, 338
Cypheliaceae, 300
Cyphelium, 300
Cyphella, 363
Cytological: data of plants showing effect of x-rays, 261; methods used in study of Delphinium, 134; study of persimmon, 213
Cytology, morphology and systematic relationships of Delphinium × Belladonna Hort. ex Bergm., 113

D

Dactylina, 379
Darrow, Robert A., Lichen collection of, 63
Deighton, F. C., lichens collected by, 271
Delphinium, 113; character associations in establishing relationships in species, 125, *127*, *129*, 131; chromosomes of species, 132, 164, of hybrids determined by Propach, 113, 165; cytological study of, 132, *178-182*, of natural species, 136, of derived hexaploids, 150; history of, 113, 132; hybrids of the Belladonna type, 113, 121, *172*, *174*, leaf types in, *113*, pollen studies of, 124, 130; morphology of natural species, 113; satellite expression in species and hybrids, 138; seed germinability in, 155; taxonomy of natural species, 114
Delphinium × Belladonna Hort. ex Bergm., The cytology, morphology, and systematic relationships of, 113
Delphinium, 113; ajacis, 114; azureum, 117, 132; Barlowii, 120, 130; Belladonna, 113, 115, 119, 125; Belladonna type, hybrids of, 117, *118*, 146; × Belladonna Hort., origin of, 113, 117, 119, variability in, 126; Bellamosum, 140; "Blue Butterfly", 121, 124, 130; "Capri", 119; cardinale, 117; cardiopetalum, 132; chamissonis, 116; cheilanthum, 113, 115, 116, *118*, 121, 124, 126, 130, 136, *166*, *170*, var. Chauvieri, 121, var. formosum, 113, var. Hendersonii, 120, var. Middendorffii, 116; ser. Cheilanthoidea, 115; chinense, 121; "Cliveden Beauty", 124, 140, *168*; sect. Consolida, 115; subg. Consolida, 115; consolida, 114; sect. Delphinastrum, 114; sect. Delphinellum, 114; subg. Diedropetala, 115; sect. Elatopsis, 115; elatum, 114, 115, 117, *118*, 119, 121, 126, 129, 130, 132, *172*, × grandiflorum, 121, 133, "Summer Skies", 124, *176*; elatum-splendens, 121, 124; subg. Eudelphinium, 115; formosum, 115, 117, 118, 130, *168*; "Grandiflora," 117; grandiflorum, 114, 115, 117, 119, 123, 126, 130, var. chinense, *118*, 121, 133, 136, *170*, "Blue Butterfly", 121, 122, 137; gypsophilum, 133; Hanseni, 133; Hendersoni, 115, 120, 125, *166*, "Lamartine", *118*, 124, 125, 130; sect. Kolobopetala, 115; Middendorffii, 116, var. parviflora, 116; "Moerheimi", 119, 124, 125, 145; "Mrs. G. Gibson", 117; nudicaule, 117, 133; peregrinum, 114; ser. Racemosum, 115; Ruysii, 133; Smith's Belladonna, *118*, 124, 126, 140, *168*; Staphisagria, 114, 132; sect. Staphisagria, 114; "Summer Skies", 124, *176*, × grandiflorum, 123; tatsienense, 115, 117, *118*; "Tom Thumb", 124; variegatum, 133
Desmaziera, 379
Digraphis, 312; *turbulenta*, 312
Dimerella, 346
Diorygma, 323; *tinctorum*, 323
Diosypros, 211; chromosomes of, 213; history of, 211; discolor, 214; kaki, 214; lotus, 214; texana, 214; virginiana, 211, 214
Diospyros virginiana L., The distribution of, 211; clonal types, 218, *224*, *225*; dispersal by animals and birds, 217, 218; forest associations, 220; in mixed oak associations, *225*; local distribution, 214, *215*, factors affecting, *212*, 214; range of, 211, *212*
Diplogramma, 307, 333
Diplographis, 312
Diploschistes, 312

Distribution of Diospyros virginiana L., 211
Dithelopsis, 273
Dodge, Carroll William: Some lichens of tropical Africa, 271
Dyplolabia, 312; *Afzelii*, 314

E

Ecology: Bluegrass pasture almanac, 1; Distribution of Diospyros virginiana L., 211; Wildwood, a study in historical, 227
Ectographa, 326
Ectolechia, 342, 343
Elmore, Mr. and Mrs. Francis, lichen collections of, 63
Emerson, R. A.: A preliminary survey of the milpa system of maize culture as practiced by the Maya Indians of the northern part of the Yucatan Peninsula, 51
Encephalographa, 393; cerebrinella, 393
Endocoena, 379
Enterodictyon, 333
Enterostigma, 333
Ethnological races of maize, variation in cob morphology among certain, 79
Etter, Alfred G.: Bluegrass pasture almanac, 1; Wildwood—a study in historical ecology, 227
Euthelenella, sect. *Microglaena*, 275
Evernia, 379
Everniopsis, 379

F

Farriola, 300
Fissurina, 312; *Dumastii*, 312; *incrustans*, 312
Florissant, Mo., history of an estate near, 227
Flower abnormalities of plants treated with x-rays, 260
Forests in the St. Louis area, 1817-18, 230
Fossils: of Medullosa, 183; of persimmon, 211
Fouragea, 307
Fulgensia, 385
Fungi of tropical Africa, 401

G

Gage, Marilyn Amy: The cytology, morphology and systematic relationships of Delphinium × Belladonna Hort. ex Bergm., 113
Gasparrinia, 385, 389; murorum, 389
Glaucinaria, 323
Glyphis, 333, 334; cicatricosa, 334, var. pulvinata, 334; *labyrinthica*, 334, 335; *tricosa*, 334
Gophers in bluegrass pastures, 3, *30*
Graphidaceae, 311, 333
Graphidula, 318
Graphina, 311, 312, 318, 323; abstracta, 324; aethiopica, 324; ambrizensis, 324; arthothelioides, 324, 325; Brunnthaleri, 324; carneum, 323; *chlorocarpa*, 312; confertum, 323; Deightoni, 324; heterospora, 324; *incrustans*, 312; javanica, 318; Pelletieri v. macrior, 324; sect. Platygrammina, 326; sect. Platygrammodes, 311, 325; sect. Platygraphina, 326; plicatum, 323; Poitiaei, 327; pyrenuloides, 324; raddacensis, 323; rudescens, 324; serpentarium, 323; socotrana, 324; sorediella, 324, 328; straminea, 324; subhiascens, 324; turgidum, 323; ulcerata, 324, 325; varians, 324
Graphis, 308, 311; Afzelii, 312, 314; albonotata, 312; aperiens v. pruinosa, 313; aterrima, 314; betuligna, 312; brachycarpa, 313; caesia, 312; *caribaea*, 303, 318; Cerasi, 312; chlorocarpa, 312; *chrysenteron*, 327; *cicatricosa*, 334; *coccinea*, 318; comma, 313; *deducta*, 330; Deightoni, 314, 316; *dendritica*, 318; Dracaenae, 313; elegans, 312; erythrocardia, 314; exalbata, 313; guineensis, 314, 317; holoeuca, 323; hyalinella, 313; increbrior, 313; infida, 313; inusta, 323; Junghuhnii, 323; labyrinthica, 335; Limae, 313; *lynceodes*, 322; mocimbensis, 313; *Montagnei*, 327; myriocarpoides, 313; myriocarpiza, 313; nigeriensis, 313, 315; nivea, 314; ochroplaca, 313; ondensis, 313, 316, 318; oxyclada, 313, 314; pallescens, 313; palmensis, 313; Poitiaei, 323; polymorpha, 327; pulverulenta, 312; raddacensis, 323; roseotincta, 312; rufula, 312; *scalpturata*, 318, 327; Schroederi, 313; subg. *Scolaeospora* sect. *Glyphis*, 334; scripta, 311, 312; serpentina, 312; striatula, 313, var. cuspidata, 313; subintricans, 313; superans, 313; tenella, 314; Thoroldi, 313, 336; timidula, 312; triticella, 313; turbulenta, 312; *ulcerata*, 325
Grazing habits of stock, effect of, on grasses, 2
Gyalecta, 346; *plurilocularis*, 348; sect. *Secoliga*, 348
Gyalectaceae, 346
Gymnographa, 307
Gyrostomum, 340, 346

H

Haematomma, 331, 365, 370; Brassii, 370; dactylopholis, 370, 371; similis, 370; subarthonioideum, 370; vulgare, 370
Hagenia picta v. rupicola, 397

Harlan, Dr. Jack, collection of Turkish popcorns made by, 33
Harpidium, 365
Helminthocarpon, 307; pruinosum, 318
Hemithecium, 323; *chrysenteron*, 323
Henry, Mrs. J. Norman, hybrid barberry in garden of, 73
Heterangium, 198
Heterodermia, 399
Heterothecium, 361; *Berteroanum*, 361
Holothelis, 273
Horse grazing, effect of, on bluegrass pastures, 7
Huea, 384, 387
Hybridization in the evolution of natural populations, 73
Hybrids: An analysis of suspected, as illustrated by Berberis × gladwynensis, 73; of Delphinium Belladonna Hort. ex Bergm., 113; of Petunia, treated with x-rays, 259
Hymenodecton, 318
Hypochnus, 337; *rubrocinctus*, 337
Hysterina, 308

I

Icmadophila, 365
Imbricaria, 372
Ionaspis, 346, 347; **ascidioides**, 347
Irradiation, effect of, on Petunia, 259

K

Kansas: coal-ball fossils found in, 184, 189
Kuttlingeria, 385

L

Larkspurs, Garland, see Delphinium
Lathagrium, 351
Laurera, 275, 280, 286, 296; astroidella, 296; elegans, 296; madreporiformis, 296; **marginata**, 296; **nigeriensis**, 296, 297; ochroleucodes, 296; pauperrima, 296; velata, 296
Leaf abnormalities of plants treated with x-rays, 260, morphology of, 265, *268*, *270*
Lecanactidaceae, 338
Lecanactis, 331, 338, 339; amylacea, 339; *confluens*, 318; **Deightoni**, 339; flava, 339; flavescens, 339; *leucophora*, 339; *lobata*, 339; *Montagnei* subsp. *deducta*, 340, subsp. *deducens*, 340
Lecania, 365; sect. *Platylecania*, 385
Lecaniopsis, 346
Lecanora, 355, 365; aequinoctialis, 367, 368; africana, 367, *367*; subg. Aspicilia, 348; **Brassii**, 366; callimorpha, 367; carneolutea, 348; carneosulphurea, 366; *conglobata*, 389; corallina, 367; *dactylopholis*, 371; ecoronata, 367; elatina, 370; **elmorei**, 65, *66*; subg. Eulecanorea, 366; fibrosa, 367; flavidonigrans, 367; flavidocarnea, 366; flavochracea, 367; *granifera*, 354; granulescens, 367; *haematomma*, 370; homaloplaca, 367; latericola, 367; laterigena, 366; lateritica, 366; leprosa v. carneola, 366, v. rufocarnea, 366; leucoplaca, 367; Monodorae, 366; notha, 367; sect. *Ochrolechia*, 369; pedata, 367; pleospora, 366; poliothallina, 366; polytropoides, 366; rubiniza, 367; sabulosa, 367; Sanctae-Helenae, 366; socotrana, 367; subcongruens, 367; subfusca v. ferax, 367, v. glebulosa, 367, v. leucoblephara, 367, v. melaleuca, 367; triguttulata, 367; tropica, 367; usambarensis, 366
Lecanoraceae, 365
Lecidea, 352, 353; albocincta, 354; amaniensis, 354; angolensis, 354, v. orientalis, 354; argillicola, 354; subg. Biatora, 353, 355; bogosensis, 354; *Buettneri*, 364; Cagnii, 354; caliginosa v. rhacocarpa, 354; capopensis, 354; *carnea*, 357; carneorufa, 354; cinereorubra, 353; citima, 354; endochrysea, 354; subg. Eulecidea, 353; furfurosula, 353; glauconigra, 354; *golungensis*, 359; granifera, 353, 354, v. lecanoroides, 355, v. leucotropoides, 355; gyalectoides, 354; *heteroloma*, 360; hypomeloides, 354; leptobola, 354; lithagoga, 354; microspermoides, 353, 356; mossamedana, 354; **nigeriensis**, 354, 356; nigricans, 354; olivacea v. alsodinea, 361; pannosa, 353; phaeophthalma, 354; rosella, 357; rubina, 354, 357; Sangeana, 354; sorediata, 395; tenuis, 353, 355; trachytica, 354; tuberculosa, 385; xanthinula, 354
Lecideaceae, 352, 384
Leightonia, 288; *porosa*, 290
Leiogramma, 318; *pruinosum*, 318; *punctiforme*, 318; *sericeum*, 318
Leiorreuma, 318, 327; *Lyellii*, 318; *tartareum*, 318
Leptogium scotinum, 351; turgidum, 351, 353; vesiculosum, 351
Leptorhapis, 273
Leptotrema, 340
Lethagrium, 351; *ascaridiosporum*, 351; *conglomeratum*, 351; *fasciculare*, 351; *rupestre*, 351; *turgidum*, 351
Letharia, 379
Leucogramma, 323, 326; *carneum*, 323; *confertum*, 323; *plicatum*, 323; *raddacense*, 323; *serpentarium*, 323; *turgidum*, 323

Lichen crispus, 351; floridus, 379; haemostomma, 370; lepadinus, 341; *lynceus*, 339; pallescens, 369; puniceus, 370; ruber, 348; rugosus, 308; saxatilis, 372; scriptus, 308, 312; speciosus, 400; ventosus, 370
Lichen flora of Arizona and New Mexico, A contribution to the, 63
Lichens of tropical Africa, Some, 271
Limboria, 312; *constellata*, 312; *tridens*, 312
Lithographa, 307
Lithothelium, 297
Lopadium, 352, 361; **Deightoni**, 361, 362; glaucophaeoides, 361; lecanorinum, 361; Newtonianum, 361; **nigrobrunneum**, 361, 363; pezizoideum, 361; **sepiaceum**, 361
Loxospora, 370

M

McQuade, Henry A.: Some x-ray effects in Petunia, 259
Maize: Archaeological remains of, in North America, 84, 86, in South America, 87; cob morphology of, 79; milpa system of culture as practiced by the Maya Indians of Northern Yucatan, 31; Popcorns of Turkey, 33; present-day races of, in Asia, 87, in North America, 83, in South America, 87; significance of popcorns in history of, 33; Variation in cob morphology among certain archaeological and ethnological races of, 79
Malvern B. Clopton Experimental Farm at Clarksville, Mo., 1
Mamay, Sergius H., and Henry N. Andrews: Some American Medullosas, 183
Manure, animal, in pastures, 2
Maya Indians, in northern part of Yucatan, Maize culture as practiced by, 51
Mazozia, 323
Medullosa, 183; anglica, 184, 197, var. ioensis, 186, var. thiesseni, 186; subg. anglorota, 186; distelica, 184, 186, *187*, *203*, *205*, *209*; elongata, 186; endocentrica, 186, 188, 197; **grandis**, 191, *192*, *193*, *195*, 197, *200*, *205*, *207*, *208*; heterostelica, 183, 184, *187*, 188, *190*, 191, 196, *205*, *206*; leuckarti, 198; noei, 191, 196, *209*; olseniae, 198; primaeva, 186, 188; solmsi, 198; thompsonii, 184, *185*, 188, 196, *202*, *203*, *204*
Medullosas, Some American, 183
Medusulina, 333
Megalographa, 326; *hysterina*, 327
Megalopsora, 372
Megalospora, 352
Meissneria, 296; *varia*, 296
Melampidium, 338
Melanodecton, 337; *indicum*, 337
Melanotheca, 281, 286, 290, 292; Achariana, 291, 292, 295; *Achariana* var. *angolensis*, 293, var. *obscurascens*, 295; **angolensis**, 293; **cameroonensis**, 293, 295; **nigeriensis**, 282, 293; **obscurascens**, 293; **porosa**, 293, 294; purpurascens, 292; **pusilla**, 292, 296
Melaspilea, 311, 318
Menegazzia, 372
Meristosporum, 296
Micrographa, 307
Microphiale, 346
Milpa system of maize culture, as practiced by the Maya Indians of northern Yucatan, 53
Minksia, 333
Monoblastia, 273, 287
Morphology: of Delphinium × Belladonna Hort. ex Bergm., 113; of Petunia plants treated with x-rays, 265; of the cob, variation in, among certain archaeological and ethnological races of maize, 79
Mycoblastus, 352
Mycoglaena, 274, 275
Myriostigma, 302; *candidum*, 302
Myriotrema, 342; *album*, 342; *olivaceum*, 342
Mytilidium, 401
Myxodictyon, 365
Myxotheca, 302; *hypocreoides*, 302

N

New Mexico, Arizona and, A contribution to the lichen flora of, 63
Nickerson, Norton H.: Variation in cob morphology among certain archaeological and ethnological races of maize, 79
Nigeria, lichens from, 271
North American races of maize, 105; cob morphology of, 83
Nyasaland, lichens from, 271

O

Ocellis, 342
Ocellularia, 340, 342; albescens, 343, 346; sect. *Ascidium*, 342; subg. Ascidium, 347; cavata, 343, 345; discoidea, 343; fumosa, 343; microspora, 344; mozambica, 343; myriospora, 343; sect. *Myriotrema*, 342; obturata, 342, 343; Poncinsiana, 343; porinoides, 343; **scolecospora**, 335, 343, 345; subterebrata, 343; terebrata, 345; **trypanea**, 343, 344
Ochrolechia, 365, 369; **palmicola**, 369
Omastin, H. A., lichens collected by, 271
Opegrapha, 307, 308; alboatra, 309; albocinerea, 309; *astroidea*, 339; aterula, 309; cretacea, 309, 327; cylindrica, 308; delicata, 309; depressum, 327; diophora, 308;

Dracaenarum, 309; elegans, 309; sect. Euopegrapha, 308; *faginea*, 308; frustulosa, 310; graphidiza, 309, 310, 311; humilis, 309; *illecebrosa*, 339; lepidella, 309; leptographa, 309; lichenoides, 308; loandensis, 309; *Lyellii*, 318; medusulina, 309; Menyhartii, 309; microspora, 309; mozambica, 310; **nigeriensis**, 309, 310; notha, 308; sect. Pleurothecium, 307; *Poitiaei*, 327; prosedoides, 309; prosodea, 309, 311; radiata, 303; rufa, 309; septemseptata, 309; sordida, 327; sororiella, 309; *streblocarpa*, 327; subcalcarea, 309; subgraphidiza, 310; subnothella, 309; tartarea, 318; Vainioi, 308; vermelhana, 309; vestita, 309; viridulata, 309
Opegraphaceae, 307, 333, 338
Ophioparma, 370
Oropogon, 378, 379
Oxystoma, 308; cylindrica, 308

P

Pachyphiale, 346
Paleobotany, 183
Pannoparmelia, 372
Parathelium, 282, 300
Parmelia, 372; abessinica, 375, f. glabrior, 375, f. sorediosa, 375; africana, 375; amaniensis, 375; sect. Amphigymnia, 374; asmarana, 373; caperata v. isidiophora, 375; cetrata v. subisidiosa, 373; coilocarpa, 373; concrescens, 373; coronata v. denudata, 373; ducalis, 374; ecaperata, 375; **eurycarpa**, 375; Hanningtoniana, 373; Hildenbrandtii, 375, v. ciliata, 375; homolotera v. bryophila, 373, v. hypocraea, 374; hypocrysalea, 375; subg. Hypogymnia, 372; sect. Hypotrachyna, 373; incisa, 397; isidiza, 374; laevigatoides, 373; latissima, 378; leptasca, 373; leucorhiza, 374; lobulascens, 375, v. **isidiosissima**, 374, 375, 377; Mangenoti, 373; Menyhartii, 375; modesta, 375; neirobiensis, 375; *nilgherrensis* v. *subciliaris*, 377; nitens, 375, f. isidiosa, 374; olivetorum v. esorediata, 375, v. sorediosa, 375; **orchidophila**, 373, 374; pedicellata, 375, v. subbullata, 375; sect. Physcioideae, 372; procera, 375; pseudotinctorum, 374, 375; revoluta v. ambigua, 373; Schimperi, 375; Schweinfurthii, 373, 375; Scottii, 373; sensibilis, 373; somaliensis, 375; Soyauxii, 375, 378; subcetrarioides, 375; **subciliaris**, 375, 377; tenuirima f. sorediata, 373; tiliacea v. hypoleuca, 373, v. rimulosa, 373; uberrima, 375; usambarensis, 373; vicinior v. bryophila, 373; zambesica, 375
Parmeliaceae, 372
Parmentaria, 297; Chevalieri, 286
Pastures, Bluegrass, 1, *24, 26, 28, 30*
Persimmon: distribution of the native, 211, by animals and birds, 217, 218, factors affecting, 214; habitat types, 218, *224*
Pertusaria relata, 345
Pertusariaceae, 287
Petunia, Some x-ray effects in, 259; cytological data, 261; morphological abnormalities, 260, *268, 269, 270;* pollen counts, 263
Phaeographina, 312, 326; **alata**, 328, 332; Balfourii, 327; brasiliensis, 327; caesiopruinosa, 330, v. striolata, 327; ceramia, 327; chrysenteron, 327; deducta, 327, 330; **Deightoni**, 327, 329; fuscescens, 328; **innata**, 327, 328; **leptotremoides**, 328, 331; **leucophora**, 327, 329; Montagnei, 327; mozambica, 327, 330; paucilocularis, 328; pezizoidea, 327; quassiaecola, 327; scalpturata, 318, 327; scriptitata, 327, 329; streblocarpa, 327; suffultum, 318
Phaeographis, 311, 312, 318; confluens, 318; **Deightoni**, 319, 320; dendritica, 318; dendriticella, 319; duplicans, 319; flammula, 318; **inusta**, 323, v. radians, 319; leucothallina, 319; lignatilis, 319; Lyellii, 318; lynceodes, 284, 319, 322; medusulina, 318; micrographa, 319; micrographoides, 319; navicularis, 319; **ochracea**, 319, 320; palmarum, 319; paragrapta, 319; Phyllocharis, 319; platycarpa, 319; punctiformis, 318; sericea, 318; sexlocularis, 319; **sierraleonensis**, 319, 321; subdevelans, 319; **subnivescens**, 319; **tecta**, 319, 322; tigrinella, 319; tridens, 312
Phaeotrema, 340
Phialopsis, 348
Phlyctella, 365
Phlyctidia, 365
Phlyctis, 365
Phragmopyxine, 395
Phyllophthalmara, 340
Phyllopsora, 364; brachyspora, 364; Buettneri, 364; pannosa, 364; parvifolia, 364
Phyllopsoraceae, 364
Physcia, 396; abbreviata, 397, 398; aegiliata, 397; **afra**, 397, 398; africana, 397; areolata, 397; adscensionis, 397; ascensionis, 397; dilatata, 397; endopyxinea, 397; flava, 397; isidiophora, 397; obscurella, 397, v. fusca, 397; palmarum, 397; picta v. coccinea, 397, v. flavicans, 397; Poncinsii, 397; reticulata, 397; setosa f. vitellina, 397; singularis, 397

Physcia, 372
Physciaceae, 395
Physcidia, 372
Pietzschea, 198
Pioneer Hi-Bred Corn Co., Turkish popcorns grown at, 33
Platygramma, 318; *dendriticum*, 318; *Lyellii*, 318; *suffultum*, 318
Pliarona, 326, 327; *Montagnei*, 327
Pollen of Petunia plants, effect of x-rays on, 261, 263
Polyblastia, 274
Polyblastiopsis, 272, 273, 274, 275, 280, 296; **fulva**, 275; haematochroa, 275; **linearis**, 275, 276; **pyriformis**, 275, 276; **sphaerica**, 275, 277; tropica, 275
Polystroma, 340
Popcorns of Turkey, 33
Popcorns: Turkish, 33, *46*, *48*; chromosome knobs of, 44; distribution of, *40*; list of types, 42; variations in, 34, *38*; Aegean race, *37*, 39; Asiatic race, 35, 46, *48*
Porina, 273, 278, 292; compuncta, 292
Porodothion, 292; *arthonioides*, 292
Porothelium, 292, 300; *arthonioides*, 292
Prairies around St. Louis in 1817, 130
Precipitation, effect of, on distribution of Diospyros virginiana, 213
Preliminary survey of the Milpa system of maize culture as practiced by the Maya Indians of the northern part of the Yucatan Peninsula, 51
Protoblastenia, 384
Pseudolecanactis, 338
Pseudophyscia, 399
Pseudopyrenula, 272, 273, 278, 279; bengoana, 278, 280; *composita*, 289; conica, 278; **Deightoni**, 275, 278, 279; diluta, 280; diremta, 280; *duplex* f. *simplicior*, 290; elliptica, 280; flavicans, 280; sect. Hemithecium, 280; sect. Homalothecium, 279; sect. *Holothecium*, 279; infossa, 278, 280; polyphragmia, 278; sect. Pseudacrocordia, 281; subgregaria, 280; superans, 280; subg. *Trypethelium* sect. *Bathelium*, 289, sect. *Eutrypethelium*, 290
Psora Buettneri, 364
Psorella, 365
Psoromidium, 364; *Wellingtonii*, 364
Psorothecium sect. *Bombyliospora*, 385
Ptychographa, 307, 333
Pycnographa, 333
Pyrenastrum, 297; **erumpens**, 298; **parathelioides**, 298, 299; plicatum, 297; **pruinosum**, 298; septicolare, 297
Pyrenodesmia, 385, 388; **conglobata**, 388, 389
Pyrenopsis haemaleia, 251
Pyrenula, 273, 278, 280, 342; Acaciae, 281; Alni, 281; annularis, 279; aspistea, 282; ceratina, 279; discolor, 279; discolorella, 279; eucalypta, 281, 283; Euphorbiae, 281; fuscolurida, 281, 283; sect. Fusidospora, 281; gibberosa, 281; glabriuscula, 282; Gravenreuthii, 281, 292; heteroclita, 282, 284, v. *denigrata*, 284, v. *minuscula*, 282; Limae, 282; mamillana, 282, 284; mastophorizans, 281; subg. *Melanotheca*, 292; mozambica, 281; neglecta, 279; nitida, 281; *obscurascens*, 295; obscurata, 281; ocellata, 281; oculifera, 281; parva, 281; porinoides, 279; Pupula, 279; sect. Pseudoacrocordia, 281; subaperta, 281; trombetana, 281, 282; *trypanea*, 344
Pyrenulaceae, 272, 333
Pyrgillus, 300
Pyrochroa, 318; *flammula*, 318; *javanica*, 318; *medusulina*, 318
Pyrrhographa, 318; *flammula*, 318; *javanica*, 318; *medusulina*, 318
Pyxine, 395; Adamesii, 395, 396; Chevalieri, 395; chrysantha, 395; Cocoes v. chrysantha, 395, v. congensis, 396, v. convexior, 396, v. sorediigera, 395; convexa, 396; devertens, 395; dimorpha, 395; endoleuca, 395; Meissneri v. sorediosa, 395; retirugella f. isidiigera, 395; sulphurans, 395

R

Racodium, 349
Radiation effects on Petunia: cytological, 261; on flowers, 260, *270*; on leaves, 260, 265, *268*, *270*
Ramalina, 378, 379
Ramonia, 346
Rhizocarpon, 352
Riddlea, 286, 287; **papillosa**, 287
Rinodina, 355, 390; **darrovii**, 69, *70*; *nimbosa*, 71; phaeocarpa, 71
Rudolph, Emanuel D.: A contribution to the lichen flora of Arizona and New Mexico, 63

S

Sagiolechia, 346
St. Louis area: animal population at Wildwood in, 215; bird population in, 248, 256; occurrence of Diospyros in, 214, 215, 216; prairie and timber area in 1817, 230; plant species found in, 254; tree species in, 232; Wildwood, 227

Sarcographa, 333, 335, 393; Cascarillae, 335; Cinchonarum, 335; sect. Eusarcographa, 335; labyrinthica, 284, 335; Thoroldi, 335, 336; tigrina, 335
Scaphis, 308; anfractuosa, 308; compressa, 308
Schismatomma, 338
Schistophoron, 300
Schistostoma, 341; dehiscens, 341
Sclerographis, 307, 401
Sclerophyton, 333
Secoliga, 346, 348; **Deightoni**, 348; **pluriloc**ularis, 348
Segestrella sect. *Melanotheca*, 292
Semigyalecta, 346
Sierra Leone, lichens from, 271
Siphula, 379
Skallerup, Harry R.: The distribution of Diospyros virginiana L., 211
Solenographa, 318
Solenospora, 365
Solorina, 303
South American races of maize, 35, 86
Sphaerophoropsis, 352
Sporopodium, 363
Stegobolus, 342; *Berkeleyanus*, 343
Steloxylon, 198
Stenographa, 323
Stirtonia, 301, 311
Stirtoniopsis, 301, 311
Stock, grazing habits of, 2
Sutcliffia, 197
Swine, effect of excretory behavior on bluegrass, 8
Sychnogonia, 273; *Bayrhoefferi*, 273
Synarthonia, 303
Syncesia, 337; *albida*, 337
Synechoblastus, 351
Systematic relationships of Delphinium × Belladonna Hort. ex Bergm., 113

T

Temperature, effects of, on distribution of Diospyros virginiana, 213
Thalloloma, 323
Thamnolia, 379
Thecaria, 326; *quassiaecola*, 327
Thecographa, 326; *ceramia*, 327
Thelenella fulva, 275; sect. *meristosporum*, 296
Thelocarpon, 273; sect. *Thelopsis*, 273
Thelococcus, 273
Thelographis, 326
Thelopsis, 273; flaveola, 273; inordinata, 273; rubella, 273; **selenospora**, 273, 274; subporinella, 273
Theloschisma, 318; *Eschweileri*, 318
Thelotrema, 340, 341; **cameroonensis**, 341, 342; *cavatum*, 345; foratum, 341; *microporum*, 343; *obturatum*, 342; subg. *Ocellularia*, 342; Pechuelii, 341; *porinoides*, 343; schistostomoides, 341; *subterebrata*, 343; terebrata, 344; sect. Tremotylopsis, 342; turgidulum, 341; *urceolare*, 342; varioloides, 341
Thelotremaceae, 340
Theobroma of tropical Africa, lichens growing on, 271
Thorold, C. A., lichen collection of, 271
Tomasellia, 286
Toninia, 352
Trees at Wildwood, St. Louis Co.: early descriptions, 230; in 1946, 232, 254; ages of, 234, diameters, heights and growth rates, 234, compared to witness trees, 237, density of, 239; vegetation beneath, 245
Tremotylium, 340; africanum, 340; angolense, 340
Trichophyma, 303
Triophthalmidium, 385
Trypetheliaceae, 286, 333
Trypethelium, 286, 290; **aciculare**, 290, 291; anomalum, 290, 291, 292; *anomalum* f. *leucostomum*, 292, v. *obscurascens*, 295; sect. *Bathelium*, 288; coccinatum, 290; *compositum*, 289; conglobatum, 292; *duplex* f. *simplicius*, 290; Eluteriae, 290; sect. *Eutrypethelium*, 290; **leucostomum**, 290, 292; marginatum, 289; *mastoideum*, 289; meristosporum, 290; *papillosum*, 288, 290; Perrotetii, 292; *platystomum* f. *leucostomum*, 292; *porosum*, 289, 290; *pusillum*, 296; pustulatum, 290; sphaerocephalum, 290; *Sprengelii* v. *porosa*, 290; *subalbens*, 290
Turkey, Popcorns of, 33
Turkish popcorns, 33; chromosome knobs, 44; distribution of, 40; grown in Iowa, 33; variations in, 34, 38; varieties of, 42, Aegean race, 27, Asiatic race, 36, *46*, *48*
Tylophorella, 300
Tylophoron, 300; ascidioides, 300; moderatum v. modestius, 300

U

Uganda, lichens from, 271
Urine, animal, effect of, on pasture grasses, 2, 9, *24*, *26*, *28*, *30*
Usnea, 379; abissinica, 382; acanthera, 382; aequatoriana, 381; africana, 383; albomaculata, 382; amplissima, 383; arguta, 383; *barbata* v. *florida* f. *australis*, 383;

Baileyi, 380; bicolorata, 382; Bornemuelleri, 382; cartilaginea, 381; chloreoides, 383; complanata, 380; contorta, 383; corrugata, 380; cristata, 380; decipiens, 381; distensa, 382; elata, 380; erubescens, 382; subg. Eumitria, 380; subg. Euusnea, 380; exasperata, 381; firmula, 380; flaccida, 381; flavescens, 380; Flotowii, 382; subsp. serpentaria, 382; fusca, 381; gigas, 383; gracilis, 381; Haumanii, 381; hispida, 382, 383; hispidula, 381; implicata, 380; incrassata, 381; Ledienii, 382; leprosa, 380, 383; Liechtensteinii, 380; livida, 383; Lyngei, 383; Meyeri, 382; moniliformis, 381; myrioclada, 382; obtusata, 382; ochrophora, 381; perhispidella, 380; perspinosa, 381; picta, 382; praelonga, 380; pseudocyphellata, 380; pulchella, 381; pulverulenta, 380; rugosa, 380; ruvidescens, 381; ruwenzoriana, 381; saxatilis, 381; scutata, 382; simplicissima, 381; speciosa, 380; subflorida, 382; submollis, 381; terrestris, 380; torrida, 382; trachyna, 382; trichodeodes, 383; umbrata, 383; undulata, 381; usambarensis, 381; Vainioana, 381; versicolor, 380; vesiculata, 380; Welwitschiana, 380
Usneaceae, 378
Ustalia, 303; *anguina*, 323

V

Variation: in cob morphology among certain archaeological and ethnological races of maize, 79; in Turkish popcorns, diagrams illustrating, *34*, *38*
Verrucaria *aspistea*, 318; *mamillana*, 284, 289; *guineensis*, 285; *parella*, 369; *porosa*, 290; *trypanea*, 344; *subcaerulescens*, 275
Volvaria, 341

W

Weeds: control of, in maize culture, 58; in bluegrass pastures, 13, 16, *28*
Wildwood—A study in historical ecology, 227: animals inhabiting, 245; birds and bird nests observed at, 248, 249, 256; history of area, 227; prairie and timber areas in 1817, 230; plant species found at, 254; tree population in 1946, 232, ages of, 235, sizes, 234; vegetation beneath trees, 246

X

X-ray: effects in Petunia, Some, 259; methods of irradiation, 259; visible effects, 260
Xanthocarpia, 384
Xenocladia, 198
Xylastra, 308
Xylographa, 307
Xyloschistes, 312

Y

Yucatan Peninsula, Maize culture as practiced by the Maya Indians in the northern part of the, 51

Z

Zea Mays, see Maize
Zwackhia, 308; *involuta*, 308

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